Systematic revision of Sabellariidae (Polychaeta) and their relationships with other polychaetes using morphological and DNA sequence data

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The affinities of honeycomb or sandcastle worms (Sabellariidae, Polychaeta) and other polychaetes are studied using morphological and DNA sequence data (18S rDNA, 28S rDNA, and EF-1 alpha). Maximum-parsimony analyses were performed including 20 terminals and 7155 aligned characters. The monophyly of Sabellariidae is confirmed and well supported and sister-group relationships with Spionida are suggested but only poorly supported. Phylogenetic relationships within Sabellariidae are also assessed for the first time, using morphological data. Maximum-parsimony analyses of 30 terminals and 31 characters were performed with and without weighting the less homoplasious characters. Implied weighting resolved polytomies recovered after non-weighting datasets and suggest that the established sabellariid subfamilies are not monophyletic and that the number of parathoracic segments is homoplastic. Instead, some opercular features and chaetal characters not often incorporated in descriptions are here shown to be phylogenetically informative and support some of the clades recovered. We provide a description of morphological features of sabellariid and previously related groups together with illustrations that will, we hope, be used as a baseline for further systematic and taxonomic studies in the group and as a framework for future molecular studies. Generic diagnoses and a description and a key to genera are provided.

INTRODUCTION

Sabellariids, commonly known as honeycomb or sandcastle worms, are easily recognizable by having well-constructed tubes of cemented sand grains sometimes attached to one another forming reefs, and by the presence of a developed operculum with rows of paleae that seals the entrance of the tube. The tube and the operculum provide the worm with protection from predators and desiccation and the operculum is also used to clean the opening of the tube from fouling animals, algae or other objects (Eckelbarger, 1976). Most sabellariids live in intertidal or shallow depths but there are some genera and species restricted to the continental shelf or the deep sea. Most genera seem to be cosmopolitan but species appear to be geographically restricted and show ecological and bathymetric limitations caused by specific temperature and water circulation requirements as wells as constraints in the type of substrate and sediment, characteristics necessary for settling and building their tubes (Kirtley, 1994; Bastida-Zavala & Becerril-Tinoco, 2009).

Reef-building sabellariids have been the focus of several taxonomic, biological and ecological studies due to their importance as constructors of three-dimensional structures, providing refuge and food for many invertebrate species (e.g. Pawlik, 1988a, b; Caline, Gruet & Legendre, 1992; Dubois, Retiere &

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Olivier, 2002; Sepulveda, Moreno & Carrasco, 2003; McCarthy *et al*., 2008; Fournier, Etienne & Le Cam, 2010) but few studies have dealt with the systematics of the group and none in a phylogenetic context. One of the main taxonomic contributions to this group is the worldwide taxonomic revision of the family undertaken by Kirtley in 1994. Some subsequent studies have dealt with new species descriptions or partial taxonomic revisions of certain genera (e.g. Lechapt & Kirtley, 1998; Nishi & Kirtley, 1999; Nishi & Núñez, 1999; Nishi, Kato & Hayashi, 2004; Bailey-Brock *et al*., 2007; Nishi *et al*., 2010), increasing the total number of nominal species in the family to 120 (Nishi *et al*., 2010) although no systematic revision has been undertaken.

MONOPHYLY OF SABELLARIIDAE AND ITS POSITION ON THE ANNELID TREE

Even though the monophyly of Sabellariidae has not been tested in a phylogenetic context, several notable features, such as the presence of the operculum bearing rows of paleae derived from the first two segments, the presence of the tentacular filaments on the operculum, the division of the body into four regions, and the arrangement of chaetae, common in all members of the group, have indicated its monophyly over the years. In contrast, the position and sister-group relationships of Sabellariidae with other polychaetes are still obscure (Rouse & Pleijel, 2003) and different studies have indicated its inclusion within Sabellida, Spionida, or Terebellida.

The group was initially grouped with Sabellidae and Serpulidae (Levinsen, 1883; Meyer, 1888; Hatschek, 1893; Benham, 1896) because of the arrangement of thoracic nephridial pores and the interpretation of the food-collecting organs of these three families as homologous. This relationship was also justified latterly by the chaetal inversion in the abdominal region (Knight-Jones, 1981; Fitzhugh, 1989; Rouse & Fauchald, 1997) and the innervation of the palps (Orrhage & Müller, 2005). But other studies indicated that the tentacular filaments and palps in sabellariids and radiolar crown in sabellids and serpulids have a different origin (Orrhage, 1978; Orrhage & Müller, 2005) and therefore they should not be considered as homologous. Recently, the chaetal arrangement in Sabellariidae has also been suggested as being not homologous to the sabellid–serpulid chaetal inversion pattern (Kieselbach & Hausen, 2008), providing no support for a sister-group relationship of sabellids and sabellariids. Concurrently, a phylogenetic hypothesis combining morphological and molecular data has also indicated that Sabellariidae and Sabellida (including Sabellidae

and Serpulidae) are not closely related (Rousset *et al*., 2004; Zrzavý *et al*., 2009; Capa *et al*., 2011).

Sabellariids have also been thought to be related to spionids (Meyer, 1888; Caullery, 1914). A revealing study by Dales (1962) places sabellariids within Spionida based on larval morphology and palp innervation. This relationship has also been recently suggested, after comprehensive analyses of combined morphological and molecular data (Rousset *et al*., 2004; Capa *et al*., 2011), as well as behavioural and ecophysical investigations (Amieva & Reed, 1987; Dubois *et al*., 2005).

Other authors have considered sabellariids as related to Terebellida (Savigny, 1822; Fauchald, 1977) or Terebelliformia (*sensu* Rouse & Pleijel, 2001), because of the presence of buccal tentacles (referred to tentacular filaments herein), and similarities regarding larval metamorphosis and opercular structure between sabellariids and pectinariids have been suggested (Rouse & Pleijel, 2001). The homology between the opercular structures has still to be tested (Orrhage, 2001; Bartolomaeus, Purschke & Hausen, 2005).

RELATIONSHIPS WITHIN SABELLARIIDAE

The taxonomic revision of the family Sabellariidae was undertaken by Kirtley in 1994. The result was the rearrangement of species within genera, erection of new ones, increasing the number of genera to 12, and the erection of two subfamilies, Sabellariinae and Lygdamiinae. He provided a chronological account of the confused taxonomy of the Sabellariidae from 1771 to 1994 but, unfortunately, he did not present a phylogeny of the group for testing the groupings he proposed within the family or the homology of the features he used for defining those two subfamilies. In addition, this publication is not readily available as he published it privately.

MATERIAL AND METHODS

The present study was split into two parts, each analysing different sets of data, for addressing relationships at different levels. The aim of the first set of analyses was to test the monophyly of Sabellariidae and assess sister-group relationships with other polychaetes. The second set of analyses aimed to present the first phylogenetic hypothesis for Sabellariidae and appraise the relationships among its members. Taxa, characters and methodology for each analysis are described below.

TAXA INCLUDED IN THE ANALYSES

For resolving the sister-group relationships of Sabellariidae and homologies of morphological features, a

group of polychaetes belonging to the orders Terebellida, Sabellida, and Spionida, and suggested to share some similarities or to be related to the sabellariids, were included in the analyses. The ingroup included members of Sabellariidae, Sabellidae, Serpulidae, Oweniidae, *Magelona*, Cirratulidae, Terebellidae, Ampharetidae, Pectinariidae, Spionidae, *Trochochaeta*, *Poecilochaeta*, and *Sternaspis* and was composed by 20 terminals. The sequences selected were those with phylogenetic signal for the questions needed to address herein (Halanych & Janosik, 2006) and available from GenBank. The outgroup included one Nereididae and one Polynoidae, groups rather closely related to members of the ingroup, but less closely than any of the ingroup members is to each other, according to latest phylogenetic hypotheses. Morphological features were scored from the literature and direct observation of material if available.

For resolving relationships among sabellariids, 30 species belonging to the 12 sabellariid genera (Kirtley, 1994) and including all type species were included in the data matrix, in order to incorporate the morphological variability within each genus and selecting those species that we could access material for (Table 1) or those which had detailed descriptions in the literature. The outgroup was that recovered as sister-group of Sabellariidae on the first analyses.

In the Systematic account, a diagnosis, description and remarks of the genera are given according to the material and literature examined. Some amendments to previous descriptions have been made and are commented on in the Remarks. The list of synonymies reflects only those reviewed and should not be considered as a detailed taxonomic revision.

MORPHOLOGICAL CHARACTERS AND CHARACTER DISTRIBUTIONS

The morphological features selected for assessing relationships at family level were scored from the literature (e.g. Dales, 1962; Orrhage, 1980; Bartolomaeus, 1995, 1998; Purschke, 1997, 2005; Hausen & Bartolomaeus, 1998; Rouse, 2000a, b; Zhadan & Tzetlin, 2003; Bartolomaeus & Quast, 2005; Eckelbarger, 2005; Hausen, 2005; Orrhage & Müller, 2005; Tzetlin & Filippova, 2005; Purschke & Müller, 2006; Purschke & Hausen, 2007; Suschenko & Purschke, 2009). The list of 99 characters and states is summarized in Table 2 and described in Appendix 1. The matrix (Table 3) was constructed in Nexus Data Editor (Page, 1998). The 'C-method' proposed by Pleijel (1995) was used for character scoring. The codification scheme included absent/present characters and unordered multistate characters. Taxa lacking the feature were scored as inapplicable and indicated as '–' and unknown as '?'.

Table 1. Material examined for scoring the sabellariid matrix

Bathysabellaria neocaledoniensis Lechapt & Gruet, 1993, New Caledonia, SW Pacific, paratype, MNHN POLY TYPE 1174.

Bathysabellaria spinifera Lechapt & Kirtley, 1996, New Caledonia, SW Pacific, paratype, MNHN POLY TYPE 1204.

Gunnarea gaimardi (Quatrefages, 1866), Cape of Good Hope, holotype, MNHN POLY TYPE 588.

Idanthyrsus australiensis (Haswell, 1883), Australia, Queensland, Thursday Island, type? BMNH 1882.2.22.71.

***Idanthyrsus* sp. nov. 1**, Christmas Island, Indian Ocean, WAM 359-75.

***Idanthyrsus* sp. nov. 2**, Australia, Western Australia, WAM 394-75.

Lygdamis augeneri Augener, 1927, Australia, New South Wales, holotype, ZMH V-9569.

Lygdamis giardi (McIntosh, 1885), Australia, New South Wales, holotype, BMNH 1885.12.1.6.

***Lygdamis* sp. nov.**, Queensland, QM G.10505, QM G.10338.

Lygdamis japonicus Nishi & Kirtley, 1999, Japan, AM W.37747

Neosabellaria vitiensis Bailey-Brock *et al*., 2007, Fiji, paratypes, AM W.31026

***Phalacrostemma* sp. nov.**, Australia, New South Wales, AM W.27566, AM W.27568.

Phalacrostemma profundum Lechapt & Kirtley, 1998, New Caledonia, SW Pacific, paratypes, MNHN POLY TYPE 1198, 1199.

Phragmatopoma californica (Fewkes, 1889), USA, California, Coronado, type?, MNHN POLY TYPE 732.

Sabellaria ishikowai Okuda, 1938, Japan AM W.37748

Sabellaria issumiensis Nishi *et al*., 2010, Japan, Chiva Prefecture, paratypes, AM W.36825

Sabellaria tottoriensis Nishi *et al*., 2004, Japan Tottori Prefecture, paratypes, AM W.29058.

***Sabellaria* sp. nov. 1**, Australia, Queensland, AM W.27195, AM W.27333.

***Sabellaria* sp. nov. 2**, Australia, Northern Territory, NTM W.4798.

Tetreres robustus Lechapt & Kirtley, 1998, New Caledonia, SW Pacific, paratypes, MNHN POLY TYPE 1200, 1201.

Abbreviations: AM, Australian Museum; MNHN, Museum National d'Histoire Naturelle; NTM, Northern Territory Museum; QM, Queensland Museum; WAM, Western Australian Museum; ZMH, Zoological Museum, Hamburg;

The characters selected for assessing relationships within sabellariids were those considered as the major features to characterize and distinguish the genera and species within Sabellariidae (Kirtley,

Table 2. List of characters and states for resolving sabellariid sister-group relationships

 1. *Prostomium and peristomium fused*: (0) absent; (1) present.
 2. *Operculum formed by head and two segments*: (0) absent; (1) present.
 3. *Radiolar operculum*: (0) absent; (1) present.
 4. *Median antenna*: (0) absent; (1) present.
 5. *Lateral antennae*: (0) absent; (1) present.
 6. *Prostomial palps*: (0) absent; (1) present.
 7. *Peristomial palps*: (0) absent; (1) present.
 8. *Prostomial tentacles*: (0) absent; (1) present.
 9. *Peristomial tentacles*: (0) absent; (1) present.
10. *Segment 1 tentacles*: (0) absent; (1) present.
11. *Building organ*: (0) absent; (1) present.
12. *Anterior glandular ventral shields*: (0) absent; (1) present.
13. *Thoracic membrane*: (0) absent; (1) present.
14. *Parapodial rami*: (0) with similar structure rami; (1) unequal rami.
15. *First few segments with no appendages*: (0) absent; (1) present.
16. *Notopodia*: (0) not projecting; (1) projecting.
17. *Notopodia missing in the posterior part of the body*: (0) absent; (1) present.
18. *Neuropodia*: (0) not projecting; (1) tori; (2) projecting.
19. *Parapodial lobes*: (0) absent; (1) present.
20. *Dorsal cirri*: (0) absent; (1) present.
21. *Ventral cirri*: (0) absent; (1) present.
22. *Chaetal inversion*: (0) absent; (1) present.
23. *Notochaetal arrangement*: (0) transverse rows; (1) bundles.
24. *Neuropodial arrangement*: (0) transverse rows; (1) bundles.
25. *Second chaetal formation site forming longitudinal rows*: (0) absent; (1) present.
26. *Paleae in first segments*: (0) absent; (1) present.
27. *Spines or hooks in first segments*: (0) absent; (1) present.
28. *Aciculae*: (0) absent; (1) present.
29. *Spines*: (0) absent; (1) present.
30. *Capillaries*: (0) absent; (1) present.
31. *Compound chaetae*: (0) absent; (1) present.
32. *Hooks*: (0) absent; (1) present.
33. *Hoods in hooks*: (0) absent; (1) present.
34. *Rostrum/main fang*: (0) absent; (1) present.
35. *Capitium/teeth over main fang*: (0) absent; (1) present.
36. *Subrostrum/breast*: (0) absent; (1) present.
37. *Subrostral process*: (0) absent; (1) present.
38. *Basal process*: (0) absent; (1) present.
39. *Manubrium/handle*: (0) absent; (1) present.
40. *Length of manubrium*: (0) short (avicular); (1) long (acicular).
41. *Posterior scaphe*: (0) absent; (1) present.
42. *Cauda*: (0) absent; (1) present.
43. *Pygidial cirri*: (0) absent; (1) present.
44. *Adult prostomial eyes*: (0) absent; (1) present.
45. *Type of eyes*: (0) simple ocelli; (1) multicellular eyes.
46. *Eyes lenses*: (0) absent; (1) present.
47. *Nuchal organs*: (0) absent; (1) present.
48. *Nuchal organs position*: (0) posteriorly in prostomium; (1) pouches from the dorsal epithelium of mouth cavity; (2) base of palps.
49. *Nuchal organs structure*: (0) pits or grooves; (1) posterior projections.
50. *Histology of nuchal organs*: (0) without cuticle; (1) with cuticle.
51. *Lateral organs*: (0) absent; (1) present.
52. *Parapodial branchiae*: (0) absent; (1) present.
53. *Branchiae:* (0) only on few anterior segments; (1) on most segments along body; (2) on posterior segments.
54. *Origin of branchiae*: (0) parapodial; (1) dorsum.
55. *Circular muscles*: (0) absent; (1) present.

Table 2. *Continued*

56. *Buccal organ*: (0) absent; (1) present.
57. *Type of buccal organ*: (0) axial muscular proboscis; (1) ventral pharyngeal organ; (2) axial non-muscular proboscis.
58. *Dorsolateral ciliary folds*: (0) absent; (1) present.
59. *Jaws*: (0) absent; (1) present.
60. *Gut*: (0) strait tube; (1) straight tube with side branches; (2) loop; (3) distinct fold.
61. *Proventricle*: (0) absent; (1) present.
62. *Faecal groove*: (0) absent; (1) present.
63. *Faecal groove inversion*: (0) absent; (1) present.
64. *Gular membrane*: (0) absent; (1) present.
65. *Location of gular membrane*: (0) between segments 4 and 5; (1) between segments 3 and 4.
66. *Head kidney (trochophore nephridia or first pair of differentiated nephridia)*: (0) protonephridia; (1) metanephridia.
67. *Adult segmental nephridia*: (0) protonephridia; (1) metanephridia.
68. *Filtration structure*: (0) podocytes; (1) solenocytes; (2) terminal cell monociliated; (3) terminal cell multiciliated.
69. *Distribution of segmental organs*: (0) in most segments; (1) several anterior nephridia and posterior gonoducts; (2) one pair of anterior nephridia and posterior gonoducts.
70. *Heart body*: (0) absent; (1) present.
71. *Blood*: (0) acellular; (1) with haemocytes.
72. *Blood colour*: (0) red (with haemoglobin); (1) green (with chlorocruorin).
73. *Nervous system*: (0) subepidermal; (1) intraepidermal.
74. *Mushroom bodies (corpora pedunculata)*: (0) absent; (1) present.
75. *Reproduction*: (0) gonochoric; (1) hermaphroditic.
76. *Asexual reproduction*: (0) absent; (1) present.
77. *Fertilization*: (0) external; (1) internal.
78. *Structure of egg envelope*: (0) smooth; (1) ornamented.
79. *Brooding*: (0) absent (broadcast spawning); (1) present (including jelly masses).
80. *Discrete ovaries*: (0) absent; (1) present.
81. *Position of the ovary*: (0) anterior segments; (1) posterior segments; (2) along the body.
82. *Type of oogenesis*: (0) intraovarian oogenesis; (1) extraovarian oogenesis.
83. *Previtellogenic oocytes (extraovarian oogenesis)*: (0) leaving the ovary as individual cells; (1) leaving the ovary as clusters of cells.
84. *Sperm head*: (0) rounded; (1) elongated.
85. *Spermatophores*: (0) absent; (1) present.
86. *Spermatozegmata*: (0) absent; (1) present.
87. *Development*: (0) direct; (1) larvae.
88. *Larvae*: (0) lecithotrophic; (1) planktotrophic.
89. *Prototroch*: (0) absent; (1) present.
90. *Metatroch*: (0) absent; (1) present.
91. *Food groove*: (0) absent; (1) present.
92. *Oral brush*: (0) absent; (1) present.
93. *Akrotroch*: (0) absent; (1) present.
94. *Meniscotroch*: (0) absent; (1) present.
95. *Telotroch*: (0) absent; (1) present.
96. *Neurotroch*: (0) absent; (1) present.
97. *Apical tuft*: (0) absent; (1) present.
98. *Tube*: (0) absent; (1) present.
99. *Tube material*: (0) mucous and sediment attached; (1) calcareous.

1994: 8), although some were excluded due to high interspecific variability (e.g. ornamentation of thecae of paleae and chaetae, the number of paleae, papillae and buccal tentacles, and the shape, size and colour of the building organ). In order to translate into a matrix the complexity of paleal forms we have scored different categories, including the general shape (cylindrical, flat or concave), the shape of margins (with or without obvious denticles), the angle formed by shaft and blade (straight or geniculate), etc. After examination of specimens, other features that show variability within the group have been added to the matrix to test the phylogenetic and taxonomic usefulness and to promote their description in future taxonomic descriptions. These are the relative length of the opercular lobes, length of palps, relative length of

Table 3. Character matrix of morphological features included for resolving sabellariid sister-group relationships

		0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–99
Nereididae	Nereis	0000110000	0001010211	1011000100	10-------	0011111000	00--110010	00-0-?1000	0001007000	--0007?10	0???101??
Polynoidae	Lepidonotus	0001110000	0001010201	1011000111	00-------	0011111000	00--010011	00-0-01200	0?01?0?0?1	20?0?0??10	01010110
Magelona	Magelona	0000001000	0007210210	0000000?1	0111100011	0010-0---	10--011100	00-0-0?21?	1?00000001	1??1?01110	00000010-
Poecilochaetus	Poecilochaetus	0000001000	0001010A10	00B2100011	00-------	0011001012	1121?11100	00-0-11010	?0?070?101	?????011?0	0???101?0
Spionidae	Polydora	0002001000	0001010A10	0000100011	0111000011	0011001011	1101011100	00-0-1101?	?700000011	0101011110	000010110
Trochochaeta	Trochochaeta	00B001000	0001010010	00B2100011	00-------	00B1001012	10--012100	00-0-?121?	?700?0?101	?????011110	000010?10
Ampharetidae	Auchenoplax	0000000010	0101211100	0010010011	0100111110	0010--1100	1101111002	0??10?1211	0000000001	0110001011	??0010110
Pectinariidae	Pectinaria	1100000010	1107110100	0010010001	0100110110	1010--1100	1100111102	0??10?131?	0000007001	01B?011110	000011110
Terebellidae	Pista	1000000100	0101111100	0010000001	0101111111	0001001100	1101111102	0101001C21	1000000001	0110012?10	?20011110
	Polycirrus	1000000100	0101111100	0010000011	0101111110	0000--1100	10-1111020	1010001D110	0000001001	1100110107	??0011110
Cirratulidae	Cirriformia	0000000000	0000700000	0000000011	00-------	00DB-100	0011111110	000-0-?1?21	0000010010	1110000-10	0000100-
Sternaspis	Sternaspis	0000007000	0007207000	0072000011	00-------	0001000--	0121110702	00-0-?1220	0000000001	?1?0?0?0?0	??000010-
Oweniidae	Owenia	1000070700	0007200000	0010000071	0100101011	0000--0---	00--011100	0100-01D?0	0000?00?1	?100?01111	100001110
Serpulidae	Hydroides	1010010000	0011010200	0110000010	0101111010	0000--1100	00--10-000	0110-01C21	0010000001	2100007?11	100001111
	Protula	1010010000	0011010200	0110000010	0101111010	0000100100	00--10-000	0110-01C21	0107000007	2100007B11	100001111
	Serpula	1010010000	0011010200	0110000010	0101111010	0000--1100	00--10-000	0110-01C21	0107000010?	2100001111	100001111
Sabellidae	Bispira	1000010000	0101010200	0110000010	0101111010	0001101100	00--10-000	0110-?1020	0100010001	2100001011	?00001010
	Eudistylia	1000010000	0101010200	0110000010	0101111010	0001001100	00--10-000	0110-?1020	0100000001	?100001011	?00001010
	Schizobranchia	1000010000	0101010200	0110000010	0101111010	0001001100	00--10-000	0110-?1020	0100000001	?100001011	?00001010
Sabellariidae	Idanthyrsus	1100001001	1001010200	0010011011	010011100-	0101001200	011010-000	1100-01D20	0700000001	10-0001110	000011110
	Gunnarea	1100001001	1001010200	0010010011	010011100-	0101001200	011010-000	1100-01D20	0700000001	10-0001110	000011110
	Sabellaria	1100001001	1001010200	0010001B011	010011100-	0101001200	011010-000	1100-01D20	0700000001	10-0001110	000011110

Polymorphisms: A, 1 + 2; B, 0 + 1; C, 0 + 3; D, 0 + 2.

Table 4. List of characters and states for resolving relationships within Sabellariidae

 1. *Opercular lobes*: (0) completely fused (entire); (1) partially fused (with deep indentation in ventral margin; (2) completely divided into two free lobes.
 2. *Operculum relative length (length from mouth to opercular papillae/maximum width)*: (0) longer than wide; (1) similar or shorter than wide.
 3. *Operculum with distal end sloped posteriorly (truncated)*: (0) absent (distal disc perpendicular to longitudinal axis; (1) present (distal disc oblique to longitudinal axis).
 4. *Opercular papillae*: (0) at least twice longer than wide; (1) shorter.
 5. *Form of tentacular filaments*: (0) simple (unbranched); (1) compound (branched).
 6. *Buccal flaps*: (0) absent; (1) present.
 7. *Palps*: (0) very short (shorter than half of the operculum length, without paleae); (1) short (shorter or similar in length to operculum); (2) long (longer than operculum).
 8. *Median organ (cirrus) at the dorsal juntion of the lobes of the opercular stalk*: (0) absent; (1) present.
 9. *Arrangement of outer paleae on opercular lobes*: (0) in semicircles; (1) in spirals.
10. *Outer opercular paleae angle of shaft and blades*: (0) straight; (1) geniculate (blade and shafts forming a conspicuous angle).
11. *Blade of outer paleae*: (0) flat; (1) concave or excavated; (2) cylindrical.
12. *Lateral margins of outer opercular paleae*: (0) smooth; (1) with large pointed denticles.
13. *Distal margins of outer opercular paleae*: (0) smooth; (1) denticulated.
14. *Outer opercular paleae with a distal plume*: (0) absent; (1) present.
15. *Inner opercular paleae arrangement*: (0) giving the appearance of 1 row; (1) giving the appearance of 2 rows.
16. *Middle opercular paleae arrangement*: (0) pointing inwards, to the centre of operculum; (1) pointing outwards, outside operculum.
17. *Middle opercular paleae angle of shaft and blades*: (0) straight; (1) geniculate.
18. *Blade of middle paleae*: (0) flat; (1) concave, excavated; (2) convex.
19. *Arrangement of inner paleae*: (0) semicircles; (1) short line on the juntion of lobes; (2) line converging inner margin of lobes; (3) short line on ventrum on inner margin of lobes.
20. *Inner paleae angle of shaft and blades*: (0) straight; (1) geniculate strongly geniculate.
21. *Blade of inner paleae*: (0) flat; (1) excavated/concave; (2) cylindrical, like spines; (3) strongly convex.
22. *Nuchal spines or hooks*: (0) absent; (1) present.
23. *Tip shape of spines*: (0) straight, spines; (1) bent, hooks.
24. *Limbation of hooks*: (0) absent; (1) present.
25. *Limbation of hooks*: (0) in the convex side of hooks; (1) in the concave side of hooks.
26. *Number of pairs of cirri on neuropodia segment 1*: (0) one; (1) two; (2) three.
27. *Neurochaetae on segment one*: (0) absent; (1) present.
28. *Number of pairs of lateral lobes on segment 2*: (0) one; (1) two; (2) three; (3) four.
29. *Thoracic branchiae (segment 2):* (0) absent; (1) present.
30. *Number of parathoracic segment*: (0) three; (1) four.
31. *Parathoracic neurochaetae*: (0) with lanceolate and capillaries; (1) only capillary chaetae; (2) only lanceolate.

opercular papillae, presence and number of neuropodial cirri in segment 1, and presence, number and shape of lateral lobes between noto- and neuropodia of segment 2. A total of 31 characters and their states are listed in Table 4 and described in Appendix 2. Feature scoring was made via the DELTA System (DEscription Language for TAxonomy) (Dallwitz, 1980) to ensure consistency among generic taxonomic descriptions (Table 5).

MOLECULAR SEQUENCES

The DNA fragments selected for testing relationships between Sabellariidae and other polychaetes were three nuclear genes, namely 18S rRNA (1889 bp), 28S rRNA (3986 bp), and elongation factor 1α (EF-1α, 1140 bp). All sequences were acquired from GenBank, and they have been part of studies about deep annelid relationships (e.g. Brown *et al*., 1999; Rousset *et al*., 2004; Struck *et al*., 2007, 2008; Capa *et al*., 2011) and also at family level (e.g. Struck, Halanych & Purschke, 2005; Kupriyanova, Macdonald & Rouse, 2006) but it is the first time the present combination of taxa and genes are included in analyses for resolving relationships of Sabellariidae and other polychaetes. In some cases, sequences from two species of the same genus have been merged and considered as one terminal (Table 6).

Sequences were aligned with MAFFT version 6 (Katoh, 2008) using the very slow, iterative refine-

Table 5. Character matrix of morphological features included for resolving relationships within Sabellariidae. '?' stands for unknown and '-' for inapplicable states

	1–10	11–20	21–30	31
Spionidae	-------0--	----------	---0-1-	-
Bathysabellaria neocaledoniens	0000001101	10000---00	110--01001	1
Bathysabellaria spinifera	0101001101	10000---00	110--01201	1
Gesaia elegans	2000001100	20000---10	2110-10111	1
Gesaia fossae	2000001100	20000---10	2110-20011	1
Gunnarea gaimardii	1101100001	00100---01	10---01110	0
Idanthyrsus macropaleus	2010101100	01100---20	2110-00210	?
Idanthyrsus australiensis	2010101100	01100---20	2110-00210	2
Idanthyrsus sp. nov. 1	2011101?00	01100---20	2110-00110	2
Idanthyrsus sp. nov. 2	201?101100	01100---20	2110-00310	2
Lygdamis indicus	2010101100	00000---20	2110-01211	0
Lygdamis augeneri	2010101100	00000---20	2110-00211	0
Lygdamis giardi	2010101100	00000---20	2110-00211	0
Lygdamis sp. nov.	2011101100	00000---20	2110-00211	0
Mariansabellaria norvegicus	2000002000	20000---10	210--00101	1
Mariansabellaria harrisae	2000002000	20000---10	210--00001	1
Neosabellaria cementum	0101100001	1011111101	10---01110	0
Neosabellaria vitiensis	0101100001	1011111101	10---01110	0
Neosabellaria uschakovi	0101100001	1011111101	10---0?110	0
Paraidanthyrsus quadricornis	2101101001	01100---01	0111001110	0
Phalacrostemma cidarophillum	2100011110	20000---10	2111121111	0
Phalacrostemma profunda	2100011110	20000---10	2111121111	0
Phalacrostemma sp. nov.	2100011110	20000---10	2111101111	0
Phragmatopoma caudata	0001101001	0011101201	30---01110	0
Phragmatopoma californica	0001101001	0011101201	30---01110	0
Sabellaria alveolata	2101101101	0010111101	10---01010	0
Sabellaria ishikawai	2101101101	0011111101	10---01010	0
Sabellaria issumiensis	2101101101	0011111101	110--01010	0
Sabellaria sp. nov. 1	2101101101	0010111101	110--01010	0
Sabellaria sp. nov. 2	2101101101	0010111101	110--01010	0
Tetreres varians	1000002000	00000---30	2110-01301	1
Tetreres superbus	1000002000	00000---30	2110-01301	1
Tetreres robustus	1000002000	00000---30	2110-01401	1

ment method recommended for sequences with multiple conserved domains and long gaps (E-INS-i) for 18S rRNA and 28S rRNA and the method recommended for sequences with general homology (G-INS-i) from EF-1α, all with an offset value of 0.2.

PHYLOGENETIC ANALYSES

Molecular and morphological data were analysed independently and in combination. Merges of matrices were performed in Winclada (Nixon, 2002). Maximum-parsimony heuristic search used 10 000 replicates of random taxon addition and the tree bisection-reconnection (TBR) branch swapping algorithm, saving ten trees per replicate using TNT 1.1 (Goloboff, Farris & Nixon, 2008b). All characters were given equal weight and multistate characters were considered non-additive. Nodal support was estimated by 1000 jackknife replicates using TBR, in TNT 1.1 (Goloboff *et al*., 2008b). New technology searches, such as ratchet, drift, and tree fusing, were implemented, isolated and in combination, using TNT 1.1 (Goloboff *et al*., 2008b) performing 100 repetitions and hitting the most-parsimonious trees 20 times. Tree metrics are abbreviated as follows: tree length (TL), consistency index excluding parsimony non-informative characters in the data matrix (CI), and retention index (RI). Support values are given on the trees.

To reach a topology that better explains those characters with a better fit to the cladistic hypothesis, at the expense of the more homoplasious ones, we have implemented implied weighting (Goloboff, 1993, 1995, Goloboff *et al*., 2008a). With this method a higher

Table 6. List of taxa included in the phylogenetic analyses for resolving sabellariid sister-group relationships and accession numbers in GenBank

	18S	28S	EF 1-α
Lepidonotus sublevis/Lepidonotus sp.	AY894301	DQ790039	DQ813370
Nereis vexillosa	DQ790083	DQ790043	DQ813377
Auchenoplax crinita	DQ790077	DQ790026	DQ813352
Pectinaria koreni/P. gouldi	DQ790091	DQ790054	DQ813388
Pista cristata	AY611461	DQ790057	DQ813391
Polycirrus sp.	EU418858	EU418866	–
Polydora sp./*P. giardi*	AY611455	DQ790059	DQ813393
Trochochaeta sp.	DQ790097	DQ790070	DQ813408
Poecilochaetus serpens	AY569652	EU418869	–
Sternaspis scutata	AY532353	DQ790063	DQ813401
Cirriformia luxuriosa/C. tentaculata	AY611456	AY611443	DQ813355
Magelona sp.	AY611454	AY611441	–
Owenia fusiformis	AB106256	DQ790049	AB003709
Bispira porifera	HM800950	HM800989 & HM801006	–
Eudistylia vancouveri	–	DQ242574	DQ813361
Schizobranchia insignis	AY732222	AY732225	–
Hydroides ezoensis	EU184062	EU184077	–
Protula palliata/P. magnifica	DQ317124	DQ317151 & DQ318584	AB003713
Serpula watsoni	EU184057	EU184068	–
Idanthyrsus pennatus/I. australiensis	HM800960	AF185174 & AF185149	–
Gunnarea capensis	AY577892	DQ318593 & EU256544	–
Sabellaria cementarium	AY732223	AY732226	DQ813395

weight is given to those characters with less homoplasy, producing a much more resolved estimated consensus tree (Goloboff *et al*., 2008a). Results using a range of concavities (values for *k*) have been compared.
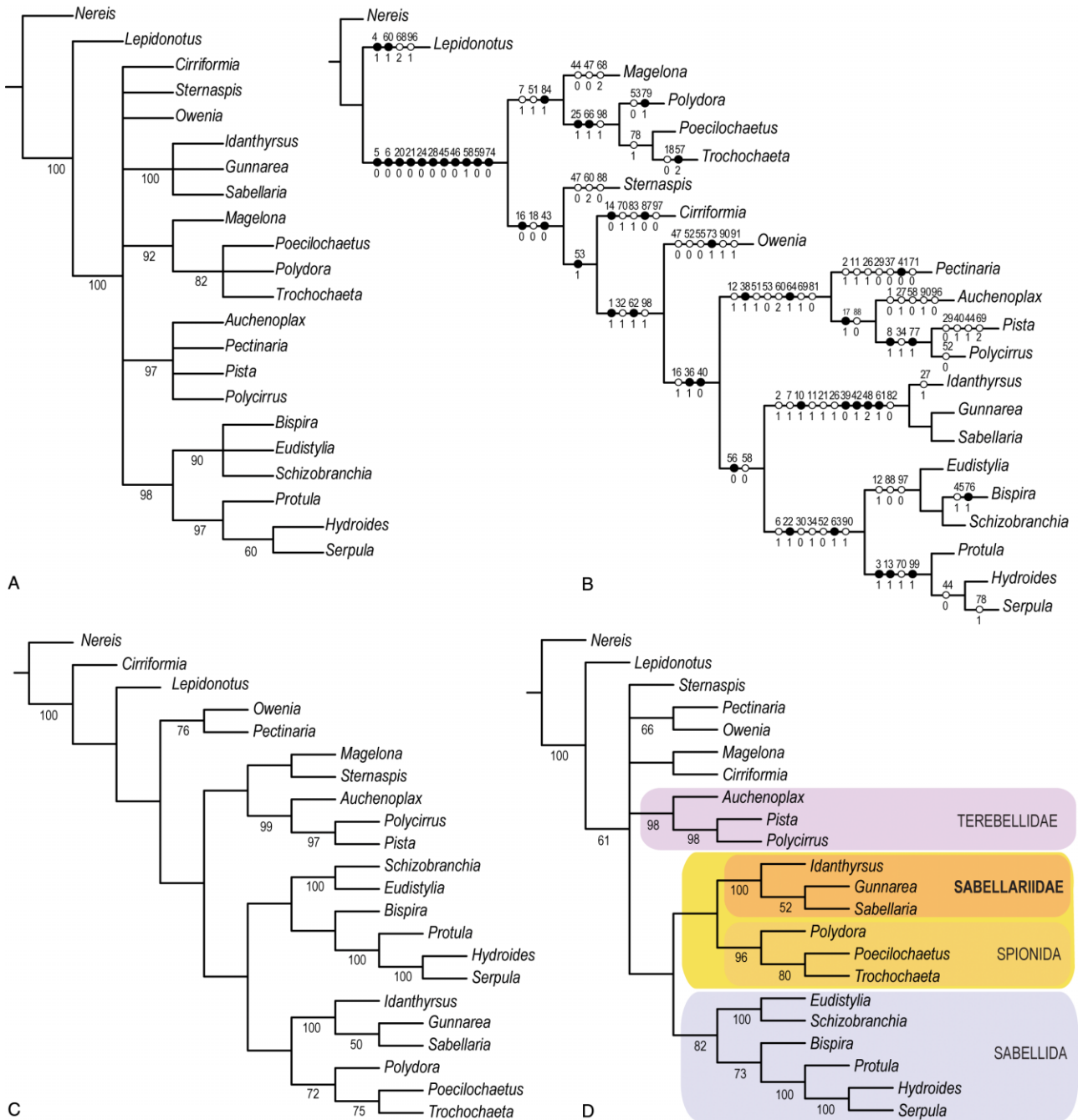
RESULTS

ANALYSES AT FAMILY LEVEL

Parsimony analysis of the morphological dataset, including 99 characters (Tables 1 and 2), 80 of which were parsimonious-informative, resulted in 25 shortest trees (TL 177, CI 0.58, RI 0.74), where Sabellariidae was recovered as monophyletic (JK 100, Fig. 1A, B) and supported by the presence of nuchal organs located at the base of palps, presence of tentacular filaments originating from segment 1, handles without a handle or manubrium in all segments, and presence of a 'proventricle' as unique synapomorphies (Fig. 1B). Other homoplastic features that support this clade are the presence of an operculum formed by the head and two anterior segments (shared with Pectinariidae), presence of a pair of peristomial palps (shared with Spionida), presence of a building organ (shared with Pectinariidae), presence of paleae in the anterior segments (shared with Pectinariidae), uncini without a rostrum or main fang (shared with Oweni-idae, Pectinariidae, and Ampharetidae), segmental branchiae inserted in the parapodia (as Pectinariidae), and intraovarian oogenesis (shared with Polynoidae) (Fig. 1B). The sister-group relationships were not resolved (Fig. 1A) although in 20 of the 25 trees Sabellariidae was closely related to Sabellida and in the other five to Terebellida.

Available sequences of 7056 nucleotides (including 1931 parsimony-informative) resulted in a unique tree (Fig. 1C) of 9215 steps (CI 0.54, RI 0.36) with four main clades, a basal clade unexpectedly gathering *Owenia* and *Pectinaria* (JK 76), a second one with *Magelona*, *Sternaspis*, and members of Terebelliformia (JK < 50), a third clade with members of Sabellida (JK < 50) including a paraphyletic Sabellidae, and a fourth clade with a monophyletic and well-supported sabellariid clade (JK 100) recovered as sister-group to Spionida (JK < 50). The position of *Cirriformia* (Cirratulidae) is surprisingly associated with the outgroup, although weakly supported.

The combination of morphological and molecular data consisted of 7155 characters, 5144 of which are variable and 2011 parsimony-informative. Results recovered two shortest trees (TL 9434, CI 0.54, RI 0.37; Fig. 1D) with the four clades also outlined in the molecular topology, although with variable relationships between them. Terebellida is recovered as paraphyletic with *Magelona* positioned as sister to *Cirriformia* and *Pectinaria* as sister to *Owenia*. Sabel-

Figure 1. Trees resulting from parsimony analyses of Sabellariidae and previously related taxa (including members of Sabellida, Terebellida and Spionida). A, strict consensus after analyses based on 99 morphological features with jackknife support values. B, first of 25 most-parsimonious trees (TL 177, CI 0.58, RI 0.74) after analyses of morphological data with unambiguous changes marked on the topology. Numbers under nodes indicate jackknife values; black dots: synapomorphies, white dots: homoplastic character states. C, shortest tree (TL 9215, CI 0.54, RI 0.36) resulting from analysis of partial 18S, 28S and EF-1α sequences with jackknife support values. D, strict consensus of two most-parsimonious trees (TL 9434, CI 0.54 RI 0.37) of the combined dataset, with jackknife support values.

lariidae was again retrieved as monophyletic (JK 100) and sister to a clade with members of Spionida (JK < 50), this being the sister clade to Sabellida (JK < 50).
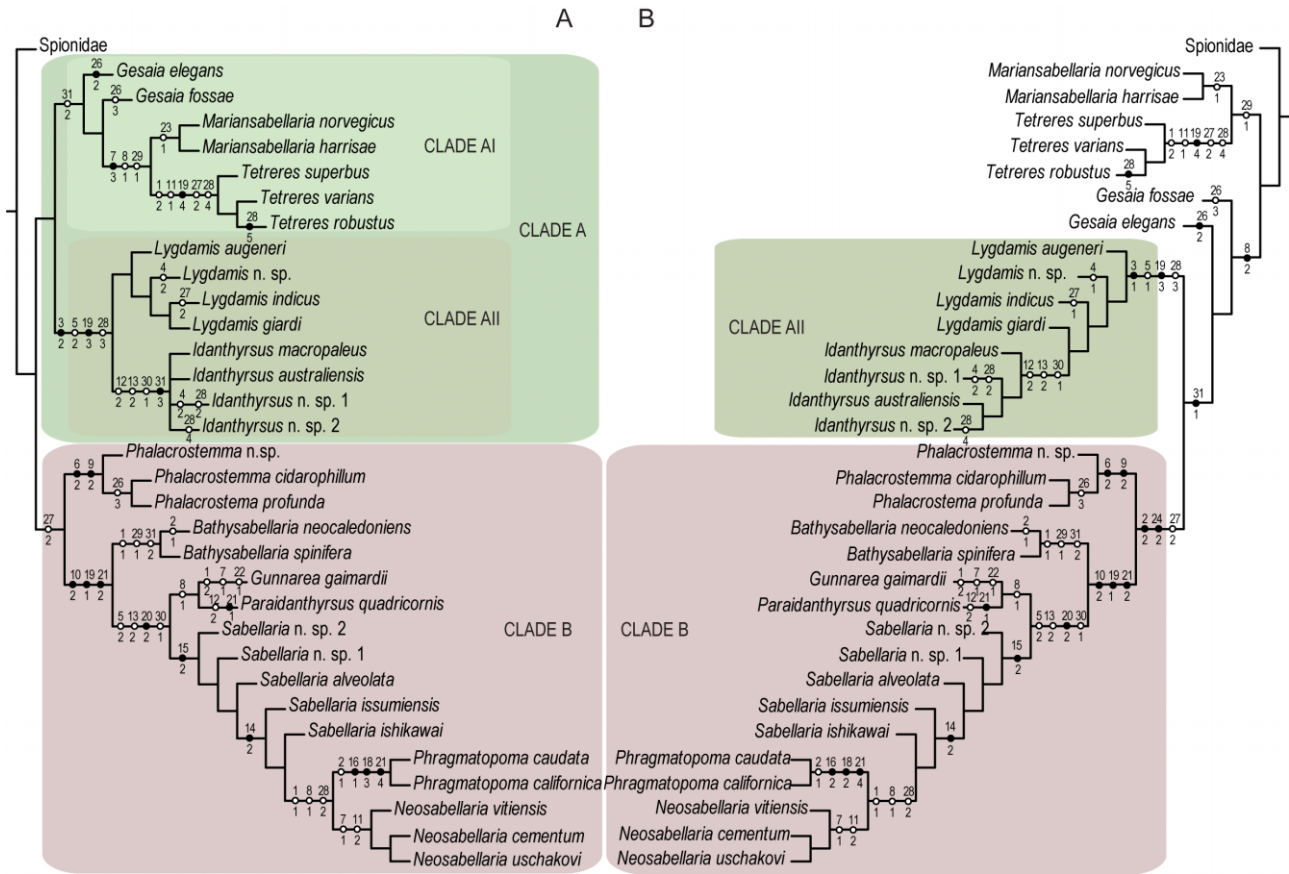
ANALYSES WITHIN SABELLARIIDAE

Maximum-parsimony analyses of 32 sabellariid species, with all the 12 genera represented by at least the type species, and 31 characters, of which 29 were parsimony-informative, resulted in 249 most-parsimonious trees (TL 73, CI 0.55, RI 0.86, Fig. 2). The trees were rooted with Spionidae as the outgroup, according to previous analyses (Fig. 1D). The polytomy at the base of the consensus tree reflects the large amount of homoplasy in the dataset for resolving bifurcating branching pattern (Fig. 2A), with only few clades being outlined, *Bathysabellaria* (JK 70), *Phalacrostemma* (JK 87), *Mariansabellaria* (JK < 50), *Tetreres* (JK 78), and a clade (JK < 50) containing a paraphyletic *Lygdamis* and *Idanthyrsus* (JK 52) (Fig. 2). Sabellariinae and Lydaminae are not recovered as monophyletic. A dataset containing only the informative characters for the type species of the 12 genera resulted in a similar topology, indicating that the specific features are not the only ones responsible for the overall homoplasy.

Implied weighting with concavity of *k* = 3 recovered three most-parsimonious trees (TL 76, CI 0.55, RI 0.86; Fig. 3A), the relationship within *Idanthyrsus* being the only difference between topologies. The monophyly of most genera are suggested except for *Gesaia* and *Sabellaria*. Two main clades are outlined and they do not fully concur with the sabellariid subfamilies. Clade A, supported by having a long operculum (lobes longer than wide), contains the genera *Idanthyrsus*, *Lygdamis*, *Tetreres*, *Mariansabellaria*, and *Gesaia*; Clade B is supported by the absence of neurochaetae on segment 1 (on both sides of the building organ) and contains *Phalacrostemma*, *Bathysabellaria*, *Paraidanthyrsus*, *Gunnarea*, *Sabellaria*, *Phragmatopoma*, and *Neosabellaria* (Fig. 3A). Within Clade A, a sister-group relationship between *Lygdamis* and *Idanthyrsus* is supported by the presence of an oblique distal end of the operculum, compound tentacular filaments, flat blades of outer paleae, and inner paleae arranged in a straight line on the inner margin of the opercular lobes, from dorsum to ventrum. Clade AI containing *Gesaia*, *Mariansabellaria*, and *Tetreres* is the sister-group to Clade AII (*Lygdamis* and *Idanthyrsus*) supported by the presence of only capillary chaetae in the neuropodia of parathoracic segments. *Mariansabellaria* and *Tetreres* are closely related based on the presence of very long palps, a median organ that appears to be absent or inconspicuous, and the absence of thoracic
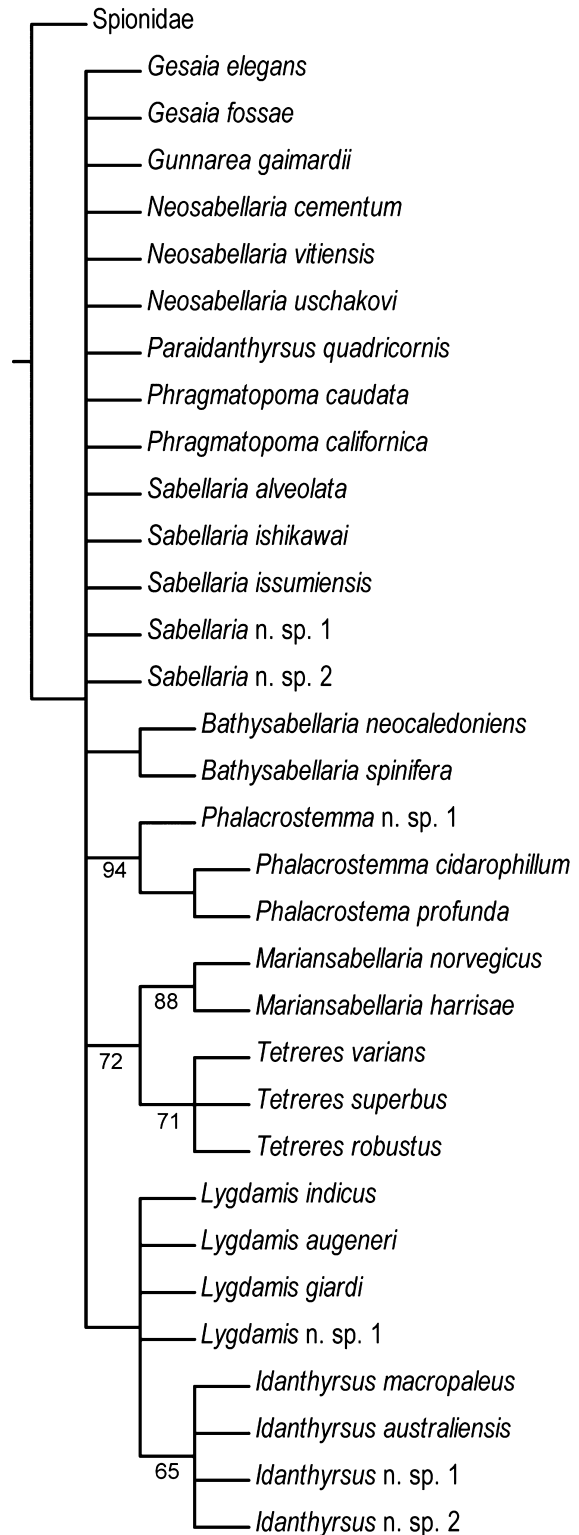
Figure 2. Strict consensus of 429 most-parsimonious trees after maximum-parsimony analysis of morphological data of members of Sabellariidae rooted with Spionidae (TL 73, CI 0.55, RI 0.86). Numbers under nodes indicate jackknife support values.

Figure 3. Trees resulting from parsimony analyses of morphological data of members of Sabellariidae and rooted with Spionidae, implementing implied weighting. Unambiguous changes are marked on the topology; black dots: synapomorphies, white dots: homoplastic character states. A, strict consensus of three most-parsimonious trees (constant of concavity $k = 3$); B, most-parsimonious tree (constant of concavity $k = 4$–6).

branchiae (in segment 2). The basal group of Clade B is *Phalacrostemma*, sister-group to all other taxa, and *Phragmatopoma* and *Neosabellaria* are recovered as a derived clade and supported by several plesiomorphies. *Paraidanthyrsus* and *Gunnarea*, two monotypic genera, are found to be closely related and sharing two plesiomorphic features but both species present several morphological differences, including different paleae, level of fusion of the opercular lobes, length of palps, and presence or absence of nuchal spines (Fig. 3A).

Similar analyses with weighting concavities of $k = 4$–6 recovered one identical most-parsimonious tree (TL 77, CI 55, RI 0.86, Fig. 2C) where Clade B is also recovered but the basal nodes of Sabellariidae differ from previous hypotheses (Figs 3B, 4). *Mariansabellaria* and *Tetreres* form a basal clade, sister to a clade with the rest of the terminals. Within this large clade *Gesaia* and two clades are recovered, Clade B and another containing *Idanthyrsus* and *Lygdamis* (Clade

AII). The monophyly of all genera is assessed except for *Gesaia*, *Sabellaria*, and *Lygdamis* (Figs 3B, 4).

Synapomorphies defining each genus are documented in the diagnoses of the taxonomic account below and two particular cases, *Gesaia* and *Sabellaria*, are discussed.

TAXONOMIC RESULTS

SABELLARIIDAE JOHNSTON, 1865

Diagnosis: Sabellariidae is characterized by some autapomorphies such as the presence of nuchal organs located at the base of palps, presence of tentacular filaments originating from segment 1; uncini without a handle or manubrium and presence of a 'proventricle'. In addition, a unique combination of the following characters (homoplastic) defines the group: the presence of an operculum formed by the head and two anterior segments, presence of a pair of
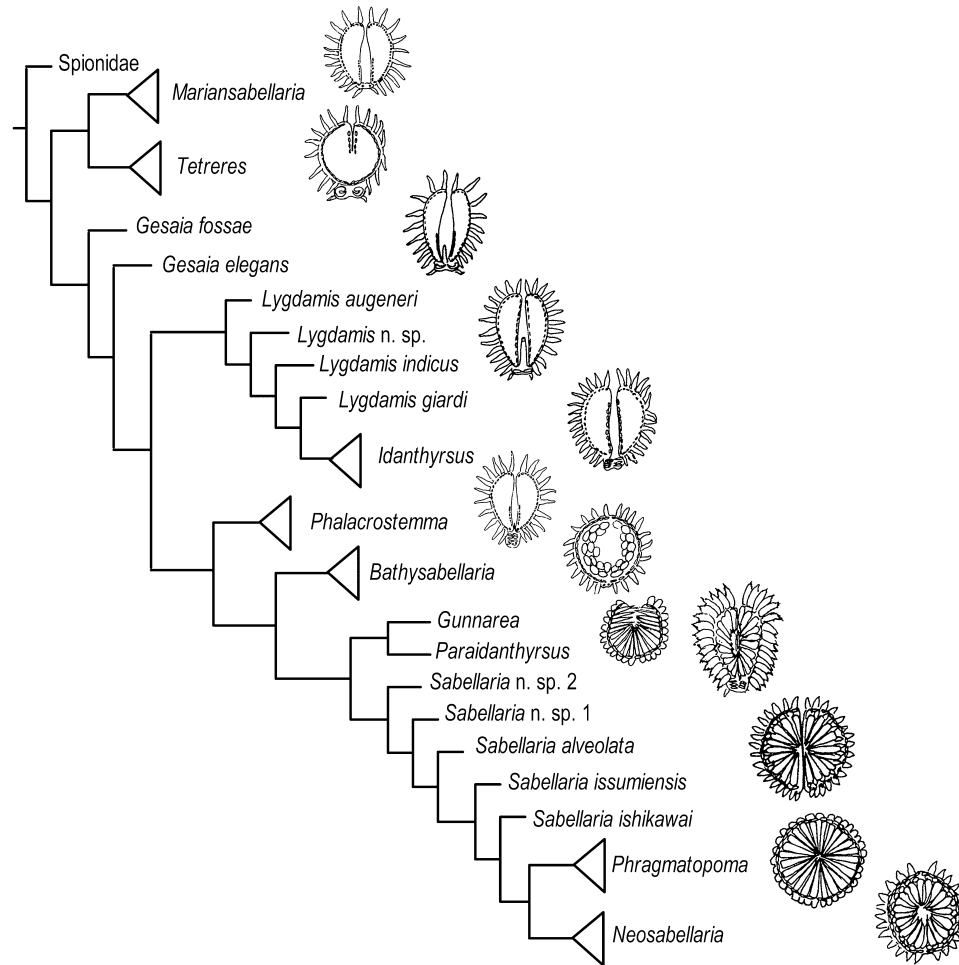
Figure 4. Schematic representation of sabellariid relationships based on maximum-parsimony analyses of the morphological data (constant of concavity $k = 4$–6) and stylized drawing of opercula from top view, modified from Kirtley (1994). See text for further details.

peristomial palps, presence of a building organ, presence of paleae in the anterior segments, uncini without a rostrum or main fang, segmental branchiae inserted in the parapodia, and intraovarian oogenesis.

Description: Body divided into four regions and consisting of an operculum (head and thorax), parathorax, abdomen, and cauda. Segmentation distinct. Operculum formed by the fusion of the prostomium, peristomium, and first two segments. Head appendages consisting of two peristomial palps; antennae absent and a median organ that sometimes protrudes from operculum edge. Prostomial ocelli present in some taxa. Nuchal organs located at base of palps. Tentacular filaments originating from segment 1 and arranged along ventral side of operculum. Building organ with horseshoe shape present and located below mouth. Parapodial rami unequal.

Parapodial lobes, dorsal and ventral cirri absent. Aciculae absent. Thoracic chaetae simple, capillaries or straight, flat, and lanceolate chaetae. Abdominal neurochaetae simple, capillaries or straight, flat, and lanceolate chaetae. Abdominal notopodia with uncini without a hood, rostrum, manubrium or basal process but with a capitium, subrostrum, and subrostral process present. Capitium consists of two lines of 6–9 teeth each. Pygidial cirri absent. Parapodial branchiae present on most segments along body. Circular muscles present and longitudinal ones grouped in bundles. Lateral organs absent. Stomodaeum without buccal organ. Gut as a straight tube, with a 'proventricle' in anterior abdominal segments. Gular membrane absent. Head kidney protonephridia and adult segmental organs, metanephridia with podocytes and terminal monociliated cells. An anterior pair of excretory and posterior gonoducts present. Circulatory system closed;

heart body absent and blood without cells. Nervous system subepidermal; brain without mushroom bodies. Species studied to date are gonochoric, broadcast spawners and with external fertilization. Females with discrete ovaries in posterior segments where oogenesis takes place. Males with rounded head sperm. Larvae planktotrophic and with prototroch, telotroch, and neurotroch ciliary bands together with an apical turf. Tube made out of mucus and sediment particles.

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KEY TO SABELLARIIDAE GENERA

1. Opercular lobes completely fused...2
Opercular lobes partially fused..4
Opercular lobes completely divided in two lobes..5
2. Outer row of opercular paleae with flattened blades...*Phalacrostemma*
Outer row of opercular paleae with cylindrical blades...3
3. Tentacular filaments simple, resembling opercular papillae. Four parathoracic segments..........*Bathysabellaria*
Tentacular filaments compound (numerous and arranged in transverse rows). Three parathoracic segments ....*Neosabellaria*
4. Outer paleae with straight blades. Tentacular filaments simple, resembling opercular papillae. Palps longer than operculum...*Tetreres*
Outer paleae geniculate, with shaft and blades forming an angle. Tentacular filaments compound (numerous and arranged in transverse rows). Palps shorter than half of length of operculum....................*Gunnarea*
5. Opercular disc (distal end) clearly oblique to longitudinal margin (e.g. Fig. 8B), with paleae arranged in a dorsal slope from lateral view...6
Opercular disc flat, with paleae arranged perpendicular to longitudinal axis (e.g. Fig. 8A)................7
6. Outer paleae with straight and flattened blades and smooth margins. Four parathoracic segments ....*Lygdamis*
Outer paleae with straight and flattened blades with large and pointed denticles on margins. Three parathoracic segments...*Idanthyrsus*
7. Blade of inner paleae cylindrical, resembling spines..8
Blades of inner paleae different (flat or concave)..10
8. Nuchal spines straight..*Mariansabellaria*
Nuchal spines with bent tips (hooks)...*Gesaia*
9. Buccal flaps present; outer paleae arranged in spirals.......................................*Phragmatopoma*
Buccal flaps absent; outer paleae arranged in semicircles...10
10. Outer paleae with flat blades and smooth margins. Nuchal spines, if present, straight and without limbations ....*Sabellaria*
Outer paleae with flat blades and large pointed denticles. Nuchal spines with bent tips (hooks) and limbation of convex side...*Paraidanthyrsus*

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BATHYSABELLARIA LECHAPT & GRUET, 1993

Bathysabellaria Lechapt & Gruet, 1993: 243, figs 1–4; Kirtley, 1994: 185.

Type species: Bathysabellaria neocaledoniensis Lechapt & Gruet, 1993, by monotypy; collected from deep water off New Caledonia.

Diagnosis: Bathysabellaria is the only group of sabellariid with the opercular lobes completely fused along its length, thoracic branchiae absent, and neuropodia of thoracic segments bearing only capillary chaetae.

Description: Operculum with lobes completely fused and with distal end (disc) flat and perpendicular to longitudinal axis. Opercular papillae numerous and digitiform. Outer paleae numerous, arranged in semicircles; shaft and blade slightly geniculate (forming an angle), blades faintly excavated, with smooth margins, except when distal tips frayed or broken. Inner opercular paleae arranged in semicircles, giving the appearance of one row, straight, slightly excavated, with smooth margins. One pair of nuchal spines, only slightly curved distally. Three or four simple (unbranched) tentacular filaments present; buccal flaps absent. Palps similar in length to operculum. With conspicuous median organ present. Neuropodia of segment 1 with one cirri on each side of building organ and capillary chaetae. Segment 2 with one pair of triangular-shaped lateral lobes. Thoracic branchiae absent. Four parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae only capillaries.

Remarks: Lechapt & Gruet (1993) erected this genus based on differences in the shape of palps and nuchal spines compared with other genera having four parathoracic segments. They also mentioned the presence of only capillaries in the neuropodia of parathoracic segments as a diagnostic feature although it was not further mentioned in redescription of the genus and description of a new species by Lechapt & Kirtley (1998). Note that the presence of capillary chaetae in parathoracic neuropodia is also present in *Mariansabellaria* (Kirtley, 1994) and at least some *Gesaia* species (Fauvel, 1911). Thoracic branchiae are absent (Lechapt & Kirtley, 1998; Figs 7, 8) although Kirtley (1994: 185) mentioned their presence and a conspicuous median organ projects from the ventral side of the opercular lobes, although it was reported as absent in the genus (Kirtley, 1994: 185). The genus contains two species only found in deep water (more than 450 m) off New Caledonia (Lechapt & Kirtley, 1998).

GESAIA KIRTLEY, 1994

Gesaia Kirtley, 1994: 166.

Type species: Phalacrostemma elegans Hartman & Fauchald, 1971: 152 (not Fauvel, 1911) designated by Kirtley (1994). Type locality: Bermuda rise, WHOI Chain Sta. 84, 36 °24.4′N, 67 °56′W; 4749 m.

Diagnosis: Monophyly of this genus has not been assessed but the species are characterized by: a long operculum divided into two lobes, with long opercular papillae, simple tentacular filaments, nuchal hooks with no limbations, branchiae on segment 2, median organ present, absence of nuchal flaps, and the presence of capillary chaetae in parathoracic neuropodia.

Description: Operculum longer than wide, completely divided into two free lobes and distal disc perpendicular to operculum; few (4–8 pairs) long and conical opercular papillae. Three to five simple (unbranched) tentacular filaments along margins of buccal cavity. Buccal flaps absent. Palps shorter or similar in length to operculum with obvious groove. Conspicuous median organ (cirrus) at dorsal junction of lobes. Outer paleae arranged in semicircles with straight, cylindrical, smooth blades (with ornamented thecae but no denticles). Inner opercular paleae arranged in a single row, like a straight line, on the dorsal half of the inner margin of lobes, with straight cylindrical and smooth paleae. One pair of nuchal spines with bent tips (hooks), without limbation. Neuropodia of segment 1 with two pairs of cirri (only described in type species) on both sides of building organ and without neurochaetae. Two lateral lobes in segment 2 (only described in type species). Thoracic branchiae

present. Four pairs of parathoracic segments. Parathoracic neurochaetae only capillaries.

Remarks: The differences between *Gesaia* and other sabellariids were not clearly stated when this genus was erected (Kirtley, 1994) and the monophyly of the genus and relationships with other sabellariids have not been assessed after phylogenetic analyses. *Gesaia* shares with *Bathysabellaria, Mariansabellaria, Phalacrostemma,* and *Tetreres* the occurrence of a long operculum with a perpendicular disc, long opercular papillae, and single tentacular filaments but only *Gesaia, Mariansabellaria,* and *Phalacrostemma* present an operculum with completely separated lobes. *Gesaia,* however, is unique among these taxa, based on the combination of the following features: presence of nuchal hooks with no limbations, branchiae on segment 2, conspicuous median organ, and absence of nuchal flaps. *Gesaia* currently contains eight species distinguished by the ornamentation of the thecae on the outer paleae. It has been reported from all the major oceans, occurring only in deep water (Kirtley, 1994).

GUNNAREA JOHANSSON, 1927

Gunnarea Johansson, 1927: 99; Kirtley, 1994: 41–42.

Type species: Hermella gaimardi (Quatrefages, 1848). From Table Bay, Cape Town, South Africa.

Diagnosis: Gunnarea is characterized by three homoplastic features: the presence of partially divided opercular lobes, very short palps, and absence of nuchal spines. An autapomorphy of this species is the presence of a broad lateral lobe on segment 2, with crenulated margins giving the appearance of being subdivided.

Description: Operculum with lobes partially fused (with deep indentation in ventral margin) and distal disc perpendicular to longitudinal axis. Numerous small and rounded opercular papillae on its perimeter. Outer paleae arranged in semicircles; geniculate, with flat blades, smooth lateral margins, and distal tooth. Inner paleae arranged in semicircles, as a single row, strongly geniculate, with flat blades. Nuchal spines absent. Palps shorter than half of the operculum. Tentacular filaments compound. Buccal flaps absent. Conspicuous median organ absent. Neuropodia of segment 1 with one cirrus on each side of building organ and capillary neurochaetae. Two triangular lobes between noto- and neuropodia of segment 2, ventral one subdivided or with crenulated margins. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate
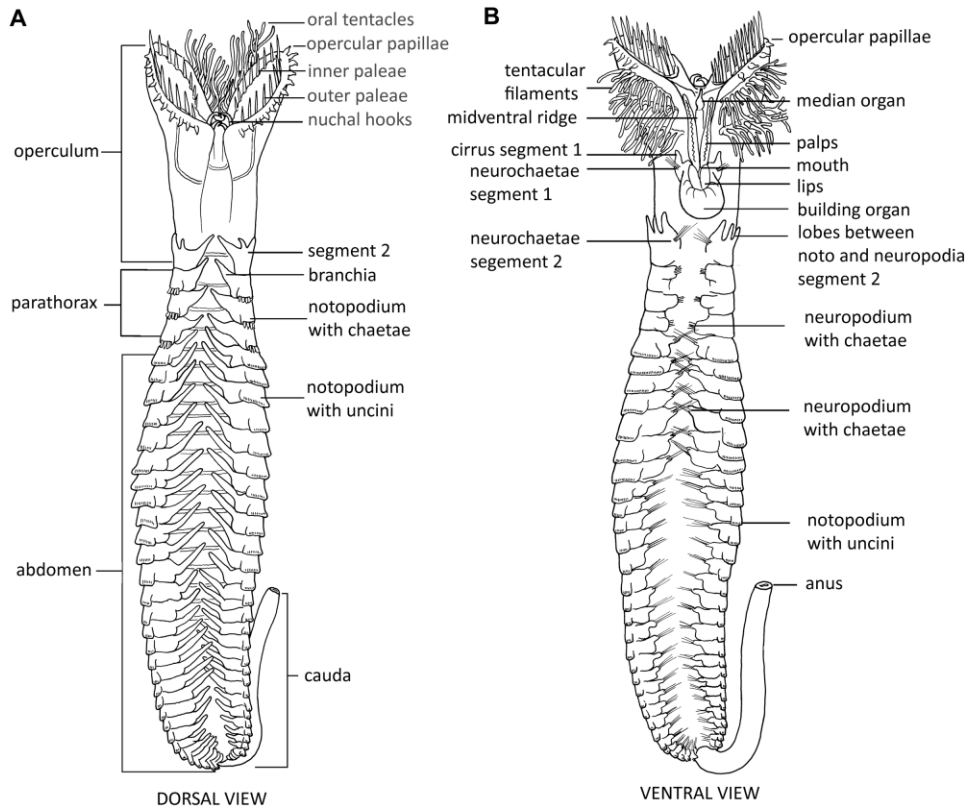
Figure 5. Stylized drawing of a sabellariid indicating the body regions and some of the morphological features described in Appendix 2: A, dorsal view; B, ventral view.
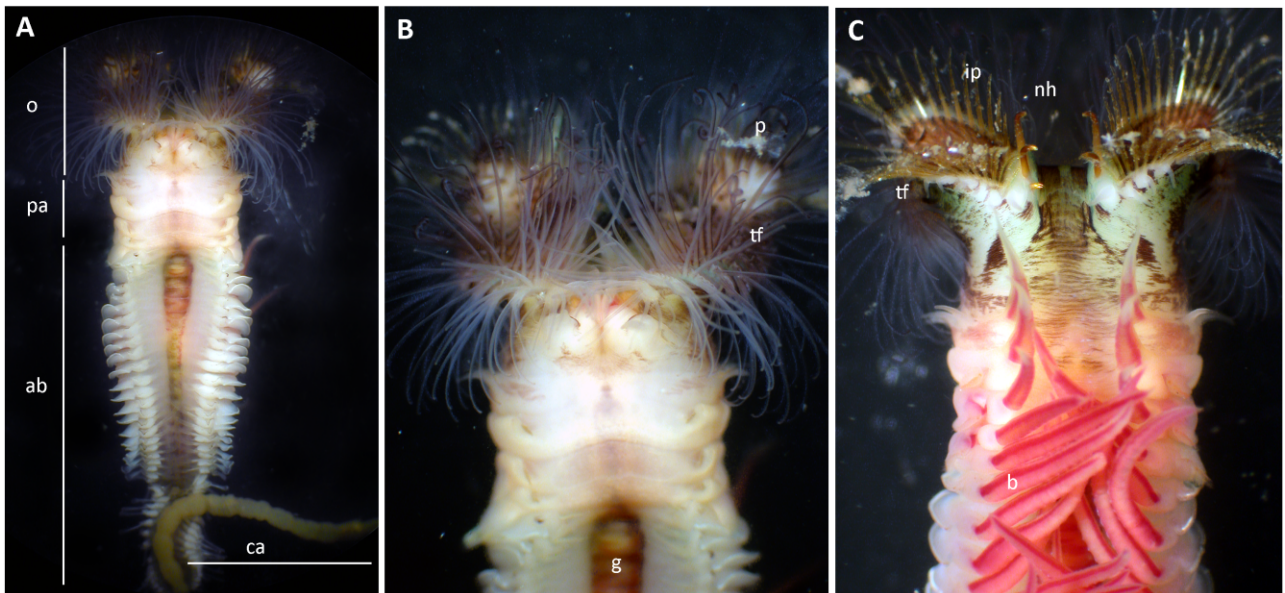
Figure 6. Photographs of *Idathyrsus australiensis* alive: A, complete specimen, dorsal view; B, anterior end, dorsal view; C, anterior end, central view. Abbreviations: ab, abdomen; b, branchia; ca, cauda; g, gut; ip, inner paleae; nh, nuchal hooks; p, paleae; o, operculum; op, outer paleae; tf, tentacular filaments; pa, parathorax.

and capillaries alternating; neurochaetae similar but smaller. Abdominal branchiae present on most abdominal segments.

Remarks: Gunnarea shares some characteristics with *Paraidanthyrsus*, *Neosabellaria*, *Sabellaria*, and *Phragmatopoma* as they all have three parathoracic segments, branching tentacular filaments, outer paleae with distal denticles and innermost row of paleae geniculate. Moreover, *Gunnarea* is recovered as sister to *Paraidanthyrsus*, supported by the absence of a conspicuous median organ, a feature that has not been checked in *Paraidanthyrsus* for the present study. *Gunnarea* is monospecific.

IDANTHYRSUS KINBERG, 1867

Idanthyrsus Kinberg, 1867: 350; Kirtley, 1994: 84.

Type species: Idanthyrsus macropaleus Schmarda, 1861 (after Kirtley, 1994). Type locality: Valparaiso Harbour, Chile.

Diagnosis: Idanthyrsus autapomorphies are outer paleae straight (no angle between shaft and blade), flat, and with pointed denticles along lateral margins and distal tips, and, if confirmed in all species of the genus, only fine lanceolate chaetae on neuropodia of parathoracic segments. Unlike other related genera they have three thoracic segments.

Description: Operculum longer than wide with lobes completely divided and distal end sloping posteriorly (oblique to longitudinal axis) and operculum papillae varying in number and size depending on species. Outer paleae arranged in semicircles with straight and flat blades and lateral and distal margins appearing sharply denticulated. Inner opercular chaetae arranged in one row along the inner margin of opercular lobes, with straight and cylindrical blades. One or two pairs of nuchal spines with bent tips (hooks) with or without limbations on the concave margin. Palps similar in length to the operculum. Median organ conspicuous with eyespots on its sides (on specimens examined). Tentacular filaments compound (branching); buccal flaps absent. Neuropodia of segment 1 achaetous, with conical cirri (one in all species examined). Segment 2 with two to four triangular lateral lobes. Three parathoracic segments with notochaetae consisting of lanceolate and capillary chaetae and only thin lanceolate neurochaetae (on specimens examined). Branchiae from segment 2 diminishing in size on posterior abdominal segments.

Remarks: All species share the presence of straight, flat, denticulated outer paleae, unique among Sabellariidae. If the presence of only lanceolate chaetae in neuropodia of parathoracic segments is confirmed in all species of the genus this would be another autapomorphy for the group. In the revision of the family, Kirtley considered *Lygdamis* and *Idanthyrsus* as belonging to different groups (subfamilies) due to the difference in number of parathoracic segments. However, analyses show that these genera are closely related as they both share the overall shape of operculum with separated and long lobes with oblique distal end, inner paleae arranged in a single line along the inner margin of lobes, and presence of nuchal hooks. Besides the number of parathoracic segments in these two groups, they differ in the shape of outer paleae (smooth in *Lygdamis*) and the presence on capillary chaetae alternating with the lanceolate neuropodia of parathoracic segments of *Lygdamis* and the latter only being present in *Idanthyrsus*. There are, at the time of writing, 19 species described in the genus (Kirtley, 1994; Nishi & Kirtley, 1999). Some features, such as the presence of limbation on nuchal hooks, presence of neurochaetae on segment 1, number of lateral lobes on segment 2, or presence of eyespots near median organ, vary between species. They are generally found in shallow water in the tropics or temperate waters as isolated individuals but some species also inhabit boreal and deep water domains and some aggregations of individuals have also been found (e.g. Kirtley, 1994; Nishi & Kirtley, 1999).

LYGDAMIS KINBERG, 1867

Lygdamis Kirtley, 1994: 116.

Type species: Lygdamis indicus Kinberg, 1867 by monotypy. Type locality: Bangka Straits, Java, Indonesia.

Diagnosis: The monophyly of the genus has not being assessed in the phylogenetic analyses although all species assigned to *Lygdamis* have an operculum with separated lobes and distal end sloped posteriorly, opercular paleae straight and smooth, the outer ones being flattened and the inner ones cylindrical, resembling spines.

Description: Operculum longer than wide with lobes completely separated and distal end sloped posteriorly (oblique to longitudinal axis). Numerous opercular papillae around edge of lobes. Outer paleae arranged in semicircles, straight, with flat blades, lateral and distal margins smooth. Inner opercular chaetae arranged in one row along the inner margin
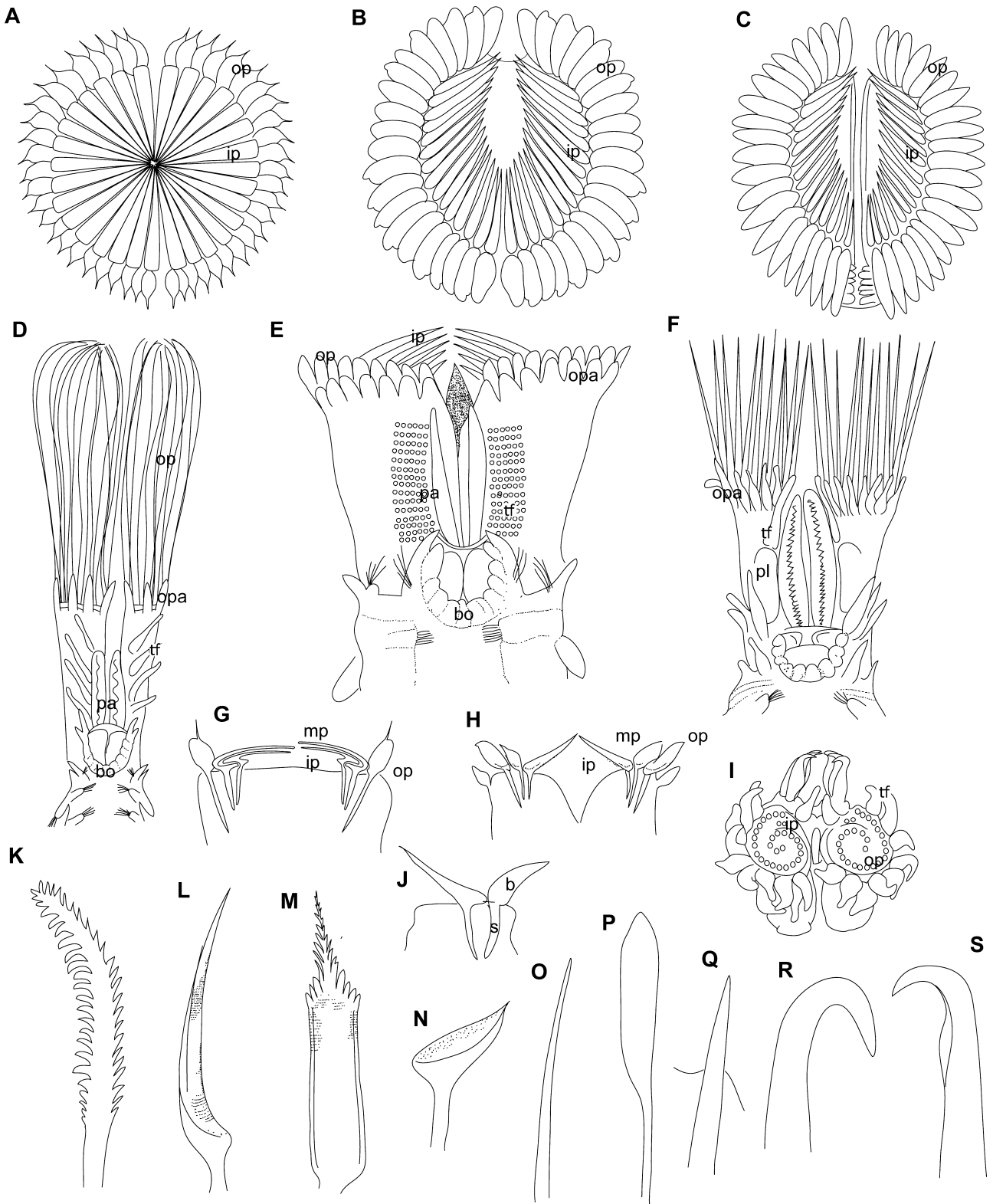
Figure 7. Stylized drawings showing morphological features described in the text: A, arrangement of opercular paleae of *Phragmatopoma* sp., upper view; B, same of *Gunnarea* sp.; C, same of *Paraidanthyrsus* sp.; D, anterior end, ventral view, *Gesaia* sp.; E, same, *Sabellaria* sp.; F, same of *Phalacrostemma* sp.; G, transverse section of the operculum showing arrangement of opercular paleae with inner row subdivided into two rows, both directed inwards; H, same, showing middle paleae directed outwards; I, outer opercular paleae in spiral arrangement; J, parts of opercular paleae; K, straight, flat blade with distal and lateral denticles, typical of outer paleae of *Idanthyrsus* spp.; L, geniculate, concave, and smooth edges of blade, typical of some middle paleae of *Sabellaria* spp.; M, straight, flat blade with distal denticles and smooth lateral edges, typical of outer paleae of *Sabellaria* spp.; N, geniculate, concave, and smooth edges of blade, typical of inner paleae of *Sabellaria* spp.; O, straight, cylindrical, and smooth blade, typical of inner paleae of *Idanthyrsus* spp.; P, straight, flat, and smooth blade, typical or inner and outer paleae of *Tetreres* spp.; Q, nuchal spine; R, nuchal spine with bent tip (hook), without limbation; S, nuchal spine with bent tip (hook), with limbation. Abbreviations: b, blade; bo, building organ; ip; inner paleae; mp, mid paleae; pa, palps; op, outer paleae; opa, opercular papillae; s, shaft; tf, tentacular filaments.

of opercular lobes with straight and cylindrical or slightly flattened blades. One pair of nuchal spines with bent tips (hooks) and without limbations. Palps similar in size to the operculum. Median organ elongate at the dorsal junction of the lobes of the opercular stalk. Tentacular filaments compound (branching); buccal flaps absent. Neuropodia of segment 1 with a conical cirrus, with or without capillary chaetae. Segment 2 with three triangular-shaped lobes between noto- and neuropodia, in some species rounded and small. Four parathoracic segments with notochaetae consisting of lanceolate and capillary chaetae and neurochaetae similar in shape but smaller. Branchiae from segment 2 to mid abdominal segments.

Remarks: According to our analyses this genus is not monophyletic but this is probably an artefact of splitting the paleal types into different categories according to their ornamentation, shape, and angle. All *Lygdamis* species have an operculum with a distal end sloped posteriorly and opercular paleae straight and smooth, the outer ones being flattened and the inner ones cylindrical. Some variation included the shape of lateral lobes of segment 2, the presence or absence of neurochaetae in segment 2, and the presence of eyes near the median organ. This genus shares several features with *Idanthyrsus* but differences are the number of parathoracic segments, the shape of outer paleae (strongly denticulated in *Idanthyrsus* and smooth in *Lygdamis*), and the presence of capillary chaetae alternating with the lanceolate chaetae on the neuropodia of parathoracic segments of *Lygdamis*, the latter type being the only ones present in *Idanthyrsus* species. The genus is known from 16 species (Kirtley, 1994).

MARIANSABELLARIA KIRTLEY, 1994

Mariansabellaria Kirtley, 1994: 136–137.

*Type species: Phalacrostemma norvegicum* Strømgren, 1971, by monotypy. Type locality: Bindalsfjiorden, Norway.

Diagnosis: Mariansabellaria is characterized by the following combination of features: presence of straight nuchal spines, very long palps, branchiae on the second segments, and the absence of a median organ. Members of the genus have a conspicuous ventral glandular area on the parathoracic segments (Kirtley, 1994), a potential autapomorphy for the group.

Description: Operculum longer than wide with lobes completely divided into two symmetrical halves and distal disc perpendicular to longitudinal axis; long conical papillae around its perimeter. Outer paleae, arranged in semicircles, smooth, straight and cylindrical or slightly flattened. Inner paleae, few in number, arranged in a short single row near the dorsal junction of margin of lobes, straiight. One or more pairs of nuchal spines. Palps grooved and longer than operculum. Tentacular filaments arranged in single rows. Buccal flaps absent. Conspicuous median organ absent. Neuropodia of segment 1 with one cirrus on each side of building organ; capillary neurochaetae absent. One or two triangular lateral lobes on segment 2. Thoracic branchiae absent. Four parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae only capillaries. Abdominal branchiae present on anterior abdominal segments but not on posterior ones.

Remarks: Mariansabellaria was characterized by the presence of conspicuous ventral glandular areas on the parathoracic segments (Kirtley, 1994) but this feature is not described in all species of the genus or in other sabellariids and therefore needs confirmation. *Mariansabellaria* shares with *Bathysabellaria*, *Gesaia*, *Phalacrostemma*, and *Tetreres* the occurrence of a long operculum with perpendicular disc, long

Figure 8. Photographs of preserved specimens: A, operculum and anterior segments, lateral view, ***Sabellaria* sp. nov. 2**; B, operculum and anterior segments, lateral view, *Lygdamis giardi*; C, detail of opercular papillae, *Lygdamis indicus*; D, head and thoracic appendices, *Idanthyrsus australiensis*; E, head and thoracic appendices, ***Sabellaria* sp. nov. 2**; F, operculum and anterior segments, ventral view, ***Phalacrostemma* sp. nov.**; G, head and thoracic appendices, *L. giardi*; H, head and thoracic appendices, *L. giardi*; I, median organ with lateral ocelli, *I. australiensis*; J, head and thoracic appendices, *Bathysabellaria spinifera*; K, operculum and paleae, dorsal view, *Tetreres robustus*; L, operculum and thoracic segments, lateral view, *B. spinifera*; M, operculum and anterior segments, lateral view, *T. robustus*. Abbreviations: b, branchia; b2, branchia segment 2; bo, building organ; cn 1, cirrus neuropodia segment 1; chn1, chaetae neuropodium segment 1; dap, dorsal papilla; es, eyespots; ip; inner paleae; li, lips; mo, mouth; mor; median organ; mr, median ridge; ns, nuchal spines (hooks); op, outer paleae; opa, opercular papillae; p, paleae; pa, palp; pl, oral plates; tf, tentacular filaments.
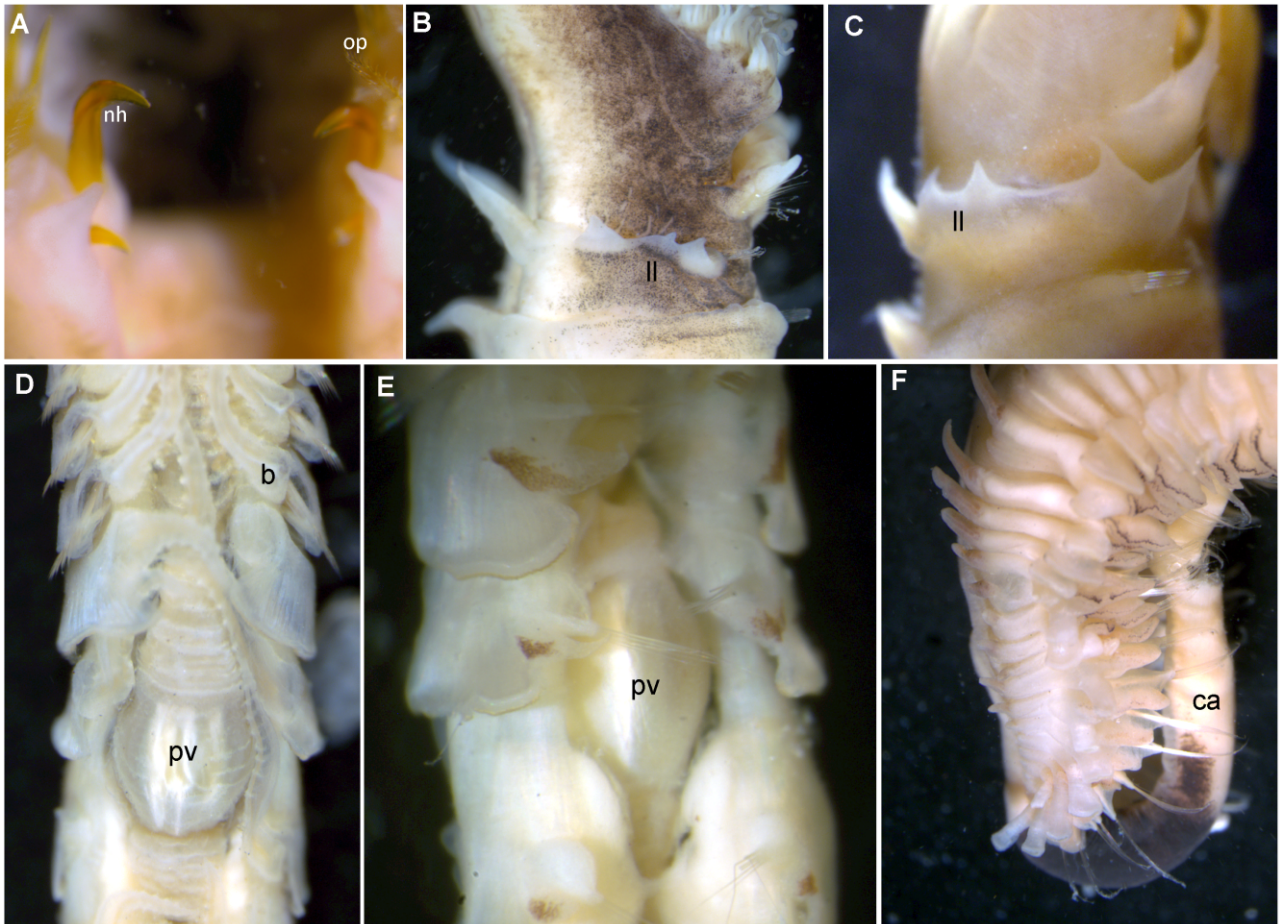
Figure 9. Photographs of preserved specimens: A, nuchal spines (hooks), *I. australiensis*; B, thoracic segments with lateral lobes, *I. australiensis*; C, thoracic segments with lateral lobes, *L. giardi*; D, abdominal segments with 'proventricle', dorsal view, ***Sabellaria* sp. nov. 2**; E, abdominal segments with 'proventricle', ventral view, ***Sabellaria* sp. nov. 2**; F, posterior abdominal segments and cauda, *Idanthyrsus australiensis*. Abbreviations: b, branchia; ca, cauda; ll, lateral lobes; nh, nuchal spines (hooks); pv, proventricle.

opercular papillae and single tentacular filaments without buccal flaps. However, only *Gesaia*, *Mariansabellaria*, and *Tetreres* have parathoracic neuropodia with just capillary chaetae. Close relationships between *Mariansabellaria* and *Tetreres* are based on the size of palps, exceeding the length of the operculum. *Mariansabellaria* is distinguished of these taxa by the presence of straight nuchal spines. This genus is represented by four species from the west coast of North and South America and also Norway, at depths ranging from 180 to 2000 m.

NEOSABELLARIA KIRTLEY, 1994

Neosabellaria Kirtley, 1994: 16; Nishi *et al*., 2010: 4.

Type species: Sabellaria cementarium Moore, 1906. From Admiralty Inlet, vininity of Port Townsend, Alaska, USA.

Diagnosis: Neosabellaria is characterized by a unique combination of characters: the presence of short palps, often not reaching half the length of the operculum and the presence of excavated outer paleae.

Description: Operculum length similar to maximum width, with lobes completely fused, although shallow mid ventral indentation sometimes present at proximal end; distal end flat and perpendicular to longitudinal axis. Numerous conical and small opercular papillae. Outer paleae numerous, arranged in semicircles, geniculate, with excavated blades, smooth lateral markings and denticulated distal margin with a midline plume. Inner opercular paleae giving the appearance of two rows. Middle paleae geniculate with excavated, smooth blades and pointed tips directed outwards, some species with rounded tipped blades also present. Innermost paleae strongly
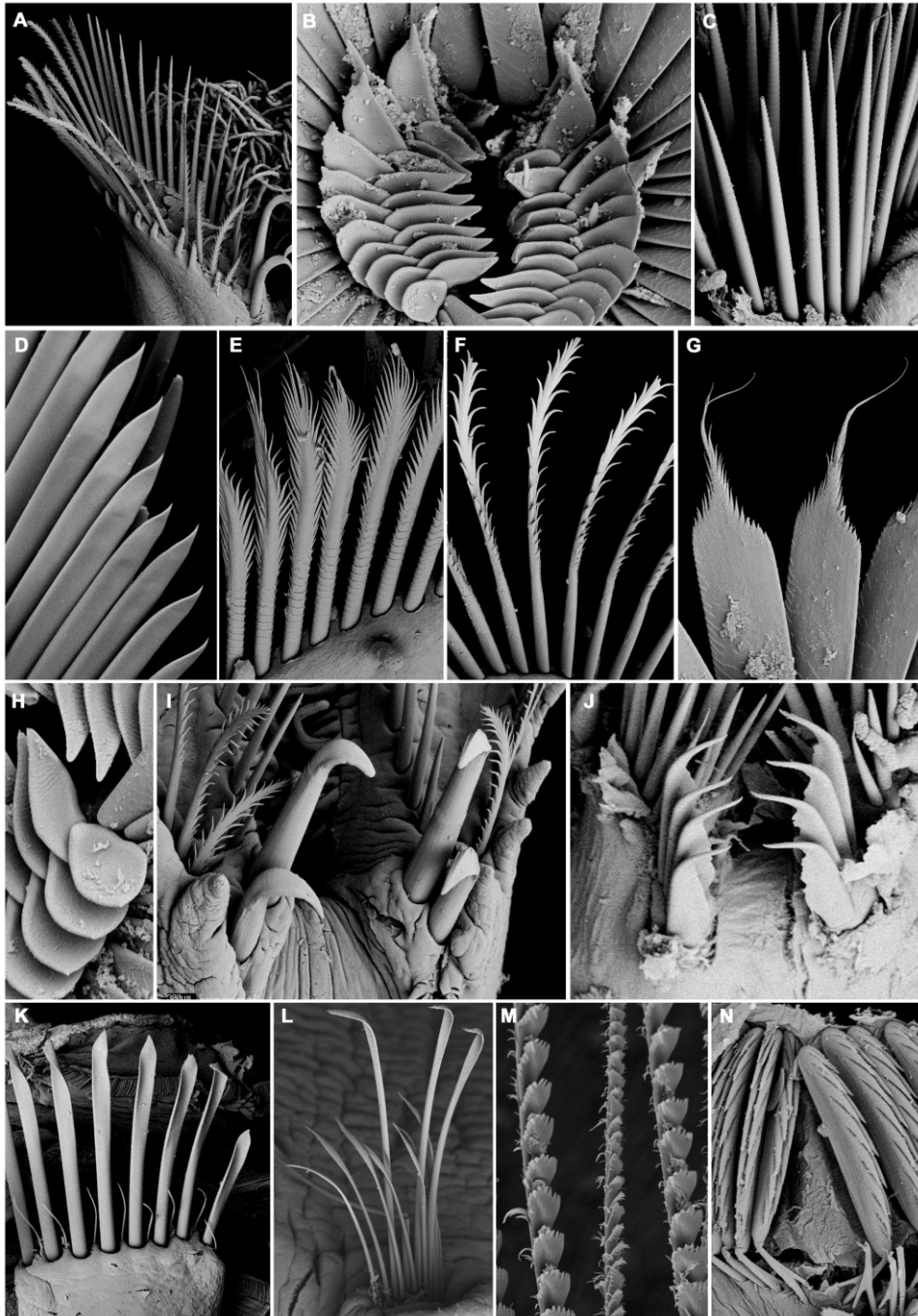
Figure 10. Scanning electron micrographs: A, arrangement of paleae in two rows, *Idanthyrsus australiensis*; B, paleae giving the appearance of being arranged in three rows with the mid and inner row directed in opposite directions, *Sabellaria* **sp. nov. 2**; C, paleae with cylindrical and straight blades, ***Phalacrostemma* sp. nov.**; D, paleae with flat, straight and smooth edges blades, *Lygdamis giardi*; E, paleae with flat, straight blades and denticulated margins, ***Idanthyrsus* sp. nov. 1**; F, paleae with flat, straight blades and denticulated margins, *Idanthyrsus australiensis*; G, paleae with flat, straight blades with smooth lateral margings but denticulated distal margins, ***Sabellaria* sp. nov. 2**; H, geniculate and concave paleae, ***Sabellaria* sp. nov. 2**; I, bent nuchal spines (hooks) without limbation *I. australiensis*; J, bent nuchal spines (hooks) without limbation *Phalacrostemma* sp.; K, parathoracic notopodia with lanceolate and capillary chaetae, *I. australiensis*; L, parathoracic neuropodia with lanceolate chaetae, of two sizes, *I. australiensis*; M, mid abdominal neurochaetae, *I. australiensis*; N, abdominal uncini with double rows of teeth, *I. australiensis*.

geniculated, with short and concave ones directed inwards. Nuchal spines absent. Compound tentacular filaments arranged in series of rows; buccal flaps absent. Palps shorter than half length of operculum. Median organ at dorsal junction of lobes of opercular stalk present but small. Neuropodia of segment 1 with one pair of cirri and capillary chaetae, at least in specimens examined. Segment 2 with two pairs of triangular-shaped lobes between noto- and neuropodia. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar in shape but smaller. Abdominal branchiae absent in posterior segments.

Remarks: Kirtley (1994) erected the genus and transferred into it previously described species of *Sabellaria* based on the complete fusion of the opercular stalk and crown whereas in *Sabellaria* they are only partially fused. *Neosabellaria*, *Sabellaria*, and *Phragmatopoma* are grouped based on the appearance of having three rows of opercular paleae, together with other character-states that are homoplastic, such as the presence of short opercular papillae, branching tentacular filaments, outer paleae geniculate and with distal denticles, innermost paleae geniculate and concave, and three parathoracic segments. *Neosabellaria* and *Sabellaria* resemble each other in the type of paleae in the middle row, as they are slightly geniculate, with excavated blades, and pointing outwards while in *Phragmatopoma* they are strongly geniculate, with convex blades and pointing inwards. However, according to our analyses *Phragmatopoma* seems to be more closely related to *Neosabellaria*, as both genera share an operculum with lobes completely fused. A key to the species of *Neosabellaria* is given by Bailey-Brock *et al*. (2007) and seven species are currently known, restricted to the Indo-Pacific.

PARAIDANTHYRSUS KIRTLEY, 1994

Paraidanthyrsus Kirtley, 1994: 80.

Type species: Hermella quadricornis Schmarda, 1861, from New Zealand.

Diagnosis: Paraidanthyrsus is characterized by the presence of geniculate outer paleae with flat blades and nuchal hooks with a limbation on the convex side.

Description: Operculum with length similar to width, lobes completely divided into two free lobes and distal disc perpendicular to longitudinal axis and numerous short papillae around its perimeter. Outer paleae arranged in semicircles, geniculate, with flat blades and margins with long and pointed denticles and

without a distal plume. Inner paleae in a single row, arranged in semicircles, strongly geniculate, with flat blades and tips directed inwards. Two or three pairs of nuchal hooks with bent tips (hooks) and limbation of the convex side. Tentacular filaments compound (branching) arranged in more than eight rows; buccal flaps absent. Palps similar in length to operculum. Conspicuous median organ at the dorsal juntion of the lobes of the opercular stalk absent. Segment 1 with a small and rounded cirrus on both sides of building organ and with capillary chaetae on the neuropodia. Segment 2 with two triangular-shaped lateral lobes. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries, similar in shape but smaller in neuropodia. Abdominal branchiae absent in posterior abdominal segments.

Remarks: In his revision of the Sabellariidae, Kirtley (1994) suggested that this monospecific genus was probably related to *Idanthyrsus* based on the presence of straight, flattened, denticulated paleae. In any of the resulting topologies *Idanthyrsus* and *Paraidanthyrsus* are recovered as sister taxa or not even in the same clades, and differently *Paraidanthyrsus* is nested within the apomorphic sabellariid as the sister-group to *Gunnarea* and basal to a clade formed by *Gunnarea*, *Neosabellaria*, *Phragmatopoma*, and *Sabellaria,* and supported by the presence of geniculate inner paleae.

PHALACROSTEMMA MARENZELLER, 1895

Phalacrostemma Marenzeller, 1895: 191; Kirtley, 1994: 147.

Type species: Phalacrostemma cidariophilum Marenzeller, 1895, by monotypy. Type locality: off Pelagossa Island, Adriatic Sea.

Diagnosis: Buccal flaps present, arrangement of outer paleae in a spiral on each lobe, in most species.

Description: Opercular width similar to length, operculum completely divided into two free lobes and distal disc perpendicular to operculum; eight to ten pairs of long and conical opercular papillae conical around lobes. Few simple (unbranched) tentacular filaments along margins of buccal cavity, absent in some species. Buccal flaps absent or present. Palps similar in length to operculum. Small median organ at dorsal junction of lobes. Outer paleae arranged in spirals with straight, cylindrical, smooth blades (with ornamented thecae but no denticles). Few (2–8) pairs of inner opercular paleae present, arranged in a straight line on the dorsal half of the inner margin of

lobes, straight, cylindrical or slightly flattened blades and smooth margins. Two to five pairs of nuchal spines with bent tips (hooks) present and limbation in the concave margin. Neuropodia of segment 1 with one to three cirri on both sides of building organ and capillary neurochaetae. Segment 2 with two digitiform lateral lobes between noto- and neuropodia. Thoracic branchiae present. Four pairs of parathoracic segments. Parathoracic notopodia with lanceolate and capillaries alternating, neuropodia with capillaries and fine lanceolate chaetae. Abdominal dorsal branchiae absent in posterior segments.

Remarks: Monophyly of *Phalacrostemma* is supported by the arrangement of outer paleae in a spiral and the presence of buccal flaps present in most species. Even though this genus shares some features such as the presence of a long operculum with perpendicular disc, long opercular papillae and single tentacular filaments with *Bathysabellaria*, *Gesaia*, *Mariansabellaria*, and *Tetreres,* it has been recovered in the base of clade B after homoplasy weighting analyses supported by the length of the operculum and the presence of neurochaetae in segment 1. *Phalacrostemma* is a cosmopolitan group represented by ten species that live solely or in aggregations at different depths. Some of these species either lack tentacular filaments (e.g. Hartman, 1944) or have only a few present, raising questions as to how they feed. Marenzeller (1904) suggested that the type species feeds by using its simple ciliated tentacular filaments on the anterior ventral margins of the operculum together with the opercular papillae.

PHRAGMATOPOMA MÖRCH, 1863

Phragmatopoma Mörch, 1863: 442.

Type species: Phragmatopoma caudata Mörch, 1863. Type locality: West Indies.

Diagnosis: Inner paleae arranged in two concentric rows, pointing inwards to the centre of the opercular disc, with strongly geniculate and convex blades, middle paleae almost covering innermost ones.

Description: Operculum longer than wide, with lobes completely fused to each other, although shallow mid ventral indentation sometimes present in proximal end. Distal disc flat and perpendicular to longitudinal axis. Numerous digitiform and long opercular papillae around its perimeter. Outer paleae numerous, arranged in semicircles; geniculate, with flat blades, smooth lateral margins, distal denticles, and a midline plume. Inner opercular paleae giving the appearance of two concentric rows, directed inwards,

with paleae strongly geniculate with convex blades and pointed tips directed inwards, middle paleae almost covering innermost paleae. Nuchal spines absent. Compound (branching) tentacular filaments arranged in series of rows; buccal flaps absent. Palps similar in length to operculum. Conspicuous median organ absent. Neuropodia of segment 1 with one conical cirri on both sides of building organ and capillary chaetae. Segment 2 with two pairs of triangular-shaped lateral lobes. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar in shape but smaller. Abdominal branchiae present to posterior segments.

Remarks: Phragmatopoma, *Neosabellaria*, and *Sabellaria* share the arrangement of inner paleae in two concentric rows. *Phragmatopoma* and *Neosabellaria* are recovered as sister groups due to the complete fusion of operculum lobes. There are four recognized species in the genus, all forming large colonies and extensive reefs in the intertidal and shallow water areas (with the exception of *P. californica* found up to 200 m) with an amphiamerican distribution (Kirtley, 1994). The type of *P. caudata* seems to be missing and the last person to see this material was Ehlers in 1901 (Kirtley, 1994). Even though no type exists, Kirtley (1994) synonymizes several species with this type species which may be premature given the original brief description.

SABELLARIA LAMARCK, 1812

Sabellaria Kirtley, 1994: 45–46; Nishi *et al.*, 2010: 7.

Type species: Sabella alveolata Linnaeus, 1767, by monotypy, collected from France?

Diagnosis: Although the monophyly of *Sabellaria* has not being assessed in our analyses, all species share the presence of an operculum completely divided into two symmetrical lobes, inner paleae arranged in two symmetrical, semicircular rows (with mid and inner paleae), and the presence of three parathoracic segments.

Description: Operculum length similar to maximum width, completely divided into two symmetrical lobes; distal disc flat and perpendicular to longitudinal axis. Numerous conical opercular papillae around operculum. Outer paleae numerous, arranged in semicircles; geniculate, with flat blades, smooth lateral edges, and smooth or denticulated distal margin and, sometimes, a midline plume. Inner opercular paleae of various shapes, giving the appearance of two rows arranged in two concentric rows. Middle paleae strongly gen-

iculate with excavated blades and smooth margins, pointing outwards; innermost paleae strongly geniculated, with short concave blades and smooth margins, directed inwards. Nuchal spines, when present, as 3–6 pairs of straight spines. Compound (branching) tentacular filaments arranged in series of rows; buccal flaps absent. Palps similar or shorter than operculum. Median organ at the dorsal juntion of the lobes of the opercular stalk conspicuous in some species and small or absent in others, with eyespots on its lateral margins in the species examined. Neuropodia of segment 1 with one pair of conical cirri and capillary chaetae. Segment 2 with one triangular-shaped lobe on both sides of building organ. Thoracic branchiae present. Three parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating; neurochaetae similar in shape but smaller.

Remarks: Nishi *et al*. (2010) have recently described a novel species of *Sabellaria* and provide a table with the chaetal characteristics of the 35 species from around the world and highlights the variability of certain features within the genus, such as the different geometry and superficial ornamentation of the paleal thecae (especially in the middle row), the presence or absence of a plume or median tooth in the outer paleae, and the presence or absence of nuchal spines. The large intraspecific variation regarding these features together with the inconsistency of the presence or absence of a median organ among *Sabellaria* species (Kirtley, 1994) compromise the assessment of the monophyly of *Sabellaria*. Nevertheless all species of *Sabellaria* share the presence of an operculum completely divided into two symmetrical lobes, inner paleae arranged in two symmetrical, semicircular rows (with mid and inner paleae), and the presence of three parathoracic segments. Branchiae on second segment (thoracic) are present (contrary to the diagnosis of Nishi *et al*., 2010). *Sabellaria* shares with *Phragmatopoma* and *Neosabellaria* the arrangement of inner paleae in two concentric rows. All species within the genus are gregarious, capable of forming large colonies and reefs along shores where suitable hydrodynamic and sedimentary conditions occur (Kirtley, 1994).

TETRERES CAULLERY, 1913

Tetreres Kirtley, 1994: 188.

Type species: Hermella varians Treadwell, 1901, designation by Kirtley, 1994. Type locality: Mayagüez Harbour, Puerto Rico.

Diagnosis: The autapomorphy that defines the group is the arrangement of the inner paleae in a short ventral line on each inner margin of the opercular lobes. Nuchal hooks are large and with broadened shafts, also unique among sabellariids.

Description: Operculum longer than wide with lobes partially fused to each other (with deep indentation on ventral margin) and distal disc perpendicular to longitudinal axis, with large conical papillae around its perimeter. Outer paleae arranged in semicircles, straight, with flat blades and smooth margins. Inner paleae few in number, arranged in a single straight row on ventral side of operculum, with straight, flattened blades. One pair of large nuchal spines, with bent tips (hooks); without limbations or enlarged shaft. Palps wrinkled and deeply grooved, longer than operculum. Tentacular filaments arranged in single rows. Buccal flaps absent. Small median organ at the dorsal junction of the lobes of the opercular stalk. Neuropodia of segment 1 with one cirrus on each side of building organ; capillary neurochaetae present. Four long, tapering lateral lobes on segment 2. Thoracic branchiae absent. Four parathoracic segments. Parathoracic notochaetae lanceolate and capillaries alternating, similar in shape but smaller in neuropodia. Abdominal branchiae present, diminishing in size posteriorly.

Remarks: Tetreres shares with *Bathysabellaria*, *Gesaia*, and *Mariansabellaria* the occurrence of a long operculum with perpendicular distal disc, long opercular papillae, and single tentacular filaments without buccal flaps. *Tetreres* is unique amongst these genera in having an operculum partially fused along its length, the arrangement of the inner paleae on the ventral-inner side of the opercular lobes and the presence of four lateral lobes (at least in the specimens examined). There are ten species within the group reported from mostly deep waters in the Atlantic, Pacific, and Southern Oceans (Kirtley, 1994).

DISCUSSION

POSITION OF SABELLARIIDAE

The monophyly of Sabellariidae, even before tested in a phylogenetic framework, has never been questioned as the group presents several morphological and developmental features unique and common to all of its members. However, its position among the annelid tree and the relationships within the family are still far from being understood. For our analyses we included available DNA information of common markers used for resolving deep-level relationships and in combination with a broad range of morphological data. Results suggest that Sabellariidae is closely related to Spionida, although support for this sister-group relationship is weak. Other authors have

also reached similar conclusions when combining morphological and molecular data regardless of the markers used (Rousset *et al*., 2004; Capa *et al*., 2011) and also after performing ecophysiological investigations (Amieva & Reed, 1987; Dubois *et al*., 2005). The organization and structure of tentacular filaments and the organization of cilia on tentacles have suggested Sabellariids to be closer to Spionids and Terebellids than Sabellids (Dubois *et al*., 2005). Our hypothesis also suggests that Spionida is polyphyletic (as in Rousset *et al*., 2004) with *Magelona* recovered as closely related to Cirratulidae. The monophyly of Terebellida could also not been assessed as Pectinariidae and Oweniidae were found as sister groups. These results suggest, as in many other studies trying to address basal relationships in Annelida (e.g. Struck & Purschke, 2005; Rousset *et al*., 2007, Zrzavý *et al*., 2009), that further investigations should probably consider other markers that enlighten the explosive radiation of this group of metazoans.

If Sabellariidae is not closely related to Sabellida, the idea of the common origin of 'crown' structures and arrangement of chaetae in thoracic and abdominal segments (Rouse & Fauchald, 1997) is discarded (as Kieselbach & Hausen, 2008). It would also mean that the scaphe and cauda, the opercular structure (Hartman, 1944; Rouse & Pleijel, 2001), and the building organ (Rousset *et al*., 2004) are not homologous (as in Watson, 1928). If Terebellida and Sabellariidae are also not closely related, the head structures and the tentacles in terebellids and sabellariids also have different origins.

The suggestion that Sabellariidae is one of the most specialized groups of polychaetes (Dales, 1952) is defended herein. If the sister-group relationships with Spionidae are confirmed, that would mean that the tubiculous ancestor of this group of worms developed a complex operculum with paleae from some anterior segments that allowed them to live permanently in a tube and with associated feeding structures, such as tentacular filaments for collecting floating particles and the building organ as a specialized structure for cementing these particles with secreted gluing substances. A regionalization of the body also took place and noto-, neuropodia and associated chaetae suffered dramatic changes with respect to preceding forms.

SABELLARIIDAE RELATIONSHIPS AND CHARACTER EVOLUTION

The topologies of the unweighted characters, resulting in a consensus tree where only few clades are delineated, indicate the high amount of homoplasy accumulated in the group. A close relationship of *Idanthyrsus* and *Lygdamis*, previously considered as

members of Sabellariinae and Lygdaminae (Kirtley, 1994), respectively, recovered in both the unweighted and the implied weighted datasets suggest these subfamilies are not monophyletic, and therefore this classification should be avoided.

The implied weighting did resolve the polytomies and uncertain relationships within Sabellariidae (for other examples and discussion of the methodology, see Goloboff, 1993, Goloboff *et al*., 2008a; Ramírez, 2003). But different results are reached depending on the value given to the concavity constant. Only the groups presented in all concavities explored should be considered as firmly established (Goloboff *et al*., 2008a) and therefore the basal relationships among those members of 'Clade A' should considered as unresolved for now.

Major morphological differences among members of Sabellariidae are found in the anterior end, probably due to major adaptive variations in morphology and anatomical structure, resulted as a consequence of external applied stress caused by environmental conditions or biological interactions (Kirtley, 1994). In contrast, the posterior segments are similar in all genera and species. The number of parathoracic segments justified the erection of the two subfamilies (Kirtley, 1994), a criterion that seemed justified because this is established very early in the course of development (Bhaud & Fernández-Álamo, 2001). However, we advocate that the number of parathoracic segments is homoplastic with four segments being the plesiomorphic condition and changing to three twice during the sabellariid radiation.

The presence of short opercula, geniculate outer paleae, and inner concave paleae arranged in semicircles are apomorphic features that characterize the derived sabellariids (*Bathysabellaria*, *Gunnarea*, *Paraidanthyrsus*, *Sabellaria*, *Phragmatopoma*, *Neosabellaria*). Besides, given the lack of a phylogenetic framework, some authors predicted that *Phragmatopoma* was a derived sabellariid due to their developed paleae (Dales, 1952) and sperm shape (Eckelbarger, 1976), compared with other Sabellariidae. The relationship between *Phalacrostemma* and this group of derived sabellariids is supported by features that are not of much significance such as length of the operculum, limbation of hooks (inapplicable for most taxa), and the presence of chaetae on the neuropodia of segment 1, instead of being grouped with the taxa that show a similar opercular structure and, in our opinion, should be considered with caution.

About 20 species, predominantly of the genera *Phragmatopoma*, *Sabellaria*, and including the monospecific genus *Gunnerea*, construct colonies and reefs of aggregated tubes in the intertidal and subtidal zones of temperate and tropical coasts in many parts

of the world (Achari, 1974; Kirtley, 1974; Pawlik, 1988a, b; Pawlik & Faulkner, 1988). After the phylogenetic hypothesis presented herein we can conclude that this characteristic and the bathymetric restrictions of some of the taxa seem not to have any phylogenetic constraint.

This paper represents the first comprehensive systematic revision of the family. Combined morphological and molecular data confirm the monophyly of Sabellariidae and its close relationships with Spionida. Phylogenetic relationships within Sabellariidae have been assessed using morphological data and suggest that the established sabellariid subfamilies are not monophyletic and the proposed groups are now based on opercular and chaetal features. The descriptions of morphological features together with the illustrations will, we hope, be used as a baseline for further systematic and taxonomic studies in the group, many species of which remain poorly described.

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APPENDIX 1

Description of characters and character-states for analyses at family level

HEAD (CHARACTERS 1–3)

In the head of sabellariids, the prostomium and peristomium are partially or totally fused to one another and with the first two thoracic segments, forming an anterior operculum that seals the tube aperture. The delimitation of segments and origin of certain structures is complicated due to this fusion, although several studies dealing with the ontogeny of some species (e.g. Dales, 1952; Wilson, 1968, 1977; Eckelbarger, 1975, 1976, 1977, 1978; Orrhage, 1978; Bhaud & Fernández-Álamo, 2001) have resolved some of these issues. The operculum, the paleae, the dorsal spines and hooks, and the tentacular filaments on the inner margin of the opercular lobes are largely derived from the first segment (Dales, 1952; Wilson, 1977). The prostomium is limited to a small region in front of the mouth and the peristomium is limited to the lips, on the buccal region (Orrhage, 1978; Amieva & Reed, 1987). The prostomium is also indistinct or partially fused to the peristomium in members of Oweniidae, Pectinariidae, Serpulidae, Sabellidae, and Terebellidae (Rouse & Pleijel, 2001; Rousset *et al*., 2003; Garraffoni & Lana, 2008, 2010; Capa *et al*., 2011; Nogueira *et al*., 2010), and as in sabellariids, the head is also fused to the first two segments in Pectinariidae (Watson, 1928). Some terebellids also have the head partially fused to the first segment (Orrhage, 2001; Garraffoni & Lana, 2010; Nogueira *et al*., 2010) but there is no operculum present.

HEAD APPENDAGES (CHARACTERS 4–10)

All members of the ingroup lack antennae, with the exception of some species of *Trochochaeta* (Pettibone, 1976) that bear a small, simple antenna on the mid-posterior end of the prostomium, and Spionidae (Orrhage, 1966; Orrhage & Müller, 2005) with a middle appendix sometimes referred to as an occipital tentacle and considered to have appeared convergently (Rouse & Pleijel, 2001). *Poecilochaetus* is considered not to have antennae as the so-called median tentacle or facial tubicle has a peristomial origin

(Mackie, 1990; Blake, 1996; Rouse & Pleijel, 2001). Members of the outgroup have both median and lateral antennae.

All palps, whether emerging from the prostomium or peristomium, have been considered as homologous in previous studies because they are similarly innervated (e.g. Orrhage, 1978; Orrhage & Müller, 2005) but have here been considered as two different characters (as in Capa *et al*., 2011). Although earlier studies suggested a possible prostomial origin of palps due their unclear position just posterior to the larval prototroch in Sabellariidae (Dales, 1952), they are currently considered as peristomial (Dales, 1962; Orrhage, 1978; Amieva & Reed, 1987; Rouse & Fauchald, 1997; Rousset *et al*., 2004; Zrzavý *et al*., 2009) due to verification of being behind the cilial band. A similar arrangement of palps has been reported in members of Spionidae, *Trochochaeta*, *Poecilochaetus*, and *Magelona* (Wilson, 1982, 2000; Rouse & Pleijel, 2001). There are no neuro-anatomical indications of the presence of palps in Terebellidae, Ampharetidae, and Pectinariidade (Orrhage, 2001; Orrhage & Müller, 2005) and therefore the multiple, grooved buccal tentacles should be considered as non-homologous to the palps from other polychaetes (Garraffoni & Lana, 2010; Nogueira *et al*., 2010). The homology statement of tentacles among members of Oweniidae (e.g. Hartman, 1960; Rouse & Pleijel, 2001; Parapar, 2003, 2006) and the palps of other polychaetes is still under discussion and therefore remains herein as unknown. These structures have been interpreted as prostomial palps, relating Oweniidae to other prostomial crown-bearing families (Rouse & Fauchald, 1997) but also as a prostomial lobe crown (Rousset *et al*., 2004) and with palps absent based on Gardiner's (1978) finding of mono-ciliated epidermal cells, not shared by any other polychaetes. In *Sternaspis*, palps have been interpreted as absent (Rouse & Fauchald, 1997; Hutchings, 2000) although in some it is still debated if the appendages present in some specimens could be considered as such (Rouse & Pleijel, 2001). In cirratulids, the presence of palps has not yet been properly investigated (Orrhage & Müller, 2005) and anterior appendices seem to originate in the peristomium and probably migrate posteriorly (Rouse & Pleijel, 2001; Rousset *et al*., 2004; Zrzavý *et al*., 2009).

The term 'buccal tentacles' has been used in the literature to refer to those appendages located near the mouth that assist with the collection of food particles (e.g. Orrhage, 1978) but homology statements need to be established in several groups. The slender appendages of the lateral parts of the ventral side of the operculum of Sabellariidae, referred to as tentacular filaments, were earlier interpreted as palps homologous with those of the Spionidae

(Johansson, 1927; Binard & Jeener, 1928), as extended lateral parts of the upper lip of the mouth, according to innervation studies (Orrhage, 1978; Orrhage & Müller, 2005) or as derived from segment 1, according to developmental studies (Dales, 1952; Wilson, 1977 and herein; Char. 10). Some studies suggested that these tentacles were homologous in Terebellidae, Ampharetidae, and Pectinariidae (Holthe, 1986; Orrhage, 2001; Orrhage & Müller, 2005), although recent studies document the prostomial origin of these tentacles in terebellids and peristomial in Ampharetidae and Pectinariidae (Garraffoni & Lana, 2008, 2010; Nogueira *et al*., 2010).

Building organ and anterior glands (characters 11–12)

Sabellariids posses a glandular, U-shaped organ (Figs 1B, 3H) that surrounds the posterior and lateral margins of the mouth and which is used to construct its robust sandy tube. Captured particles are conveyed along the tentacular filaments to the building organ, where they are held and evaluated for size, shape, and composition. Suitable particles are covered with cement secreted from thoracic cement glands and then pressed into place at the end of the tube by the building organ (Eckelbarger, 1978; Stewart *et al*., 2004). The bioadhesive material secreted by some species in the family not only serves to form the tube but also provides the chemical signal that is recognized by the planktonic larvae and induce them to attach and metamorphose (Eckelbarger, 1978; Jensen, 1992). The building organ has been regarded as part of segment 1 (Rousset *et al*., 2004) and homologous to the 'cementing organ' found in *Pectinaria* (Watson, 1928) on segment 2 (Rousset *et al*., 2004). It has therefore being scored herein as such to test homology.

Anterior glands with a major role in tube formation have been described in several groups of tubiculous polychaetes (Fitzhugh, 1989; Kirtley, 1994; Vovelle, 1997; Rousset *et al*., 2003; Glasby, Hutchings & Hall, 2004; Vinn & ten Hove, 2009). The parathoracic segments in sabellariids have more or less defined glands on their ventral surfaces that are used in association with the building organ to produce cementing and fixative substances (Kirtley, 1994). By contrast, distinct ventral shields are typical for most Terebellida and Sabellida (McHugh, 1995; Vovelle, 1997; Rousset *et al*., 2004; Garraffoni & Lana, 2008) although controversy exists regarding interpretations of these glandular pads (for details see Garraffoni & Lana, 2008; Nogueira *et al*., 2010).

Parapodia (characters 14–21)

Parapodia are generally present in polychaetes and, when present, they consist of two rami, similar or unequal in size and structure, sometimes composed of several lobes (Spionidae or Nereididae). Well-developed parapodia are often supported by aciculae (as in Nereididae and Polynoidae) and always bear chaetae. In errant polychaetes, neuropodia are generally larger than notopodia while in tubiculous worms this is not always the case and the presence of glandular tori is common among them. Other distinct parapodial structures include the dorsal and ventral cirri whose presence, shape, and arrangement vary between and sometimes within families and have therefore been included in the present study.

Chaetal arrangement (characters 22–25)

Previous studies have considered the arrangement of chaetae in parathoracic and abdominal segments in sabellariids, with uncini on the notopodia of the abdominal region, as a consequence of the chaetal inversion typical of members of Sabellida (Knight-Jones, 1981; Fitzhugh, 1989; Smith, 1991; Rouse & Fauchald, 1997; Schulze, 2003; Rousset *et al*., 2004). But recent studies demonstrate that this chaetal arrangement corresponds to different processes and are not homologous (Kieselbach & Hausen, 2008).

In many sedentary polychaetes chaetae are arranged in transverse rows perpendicular to the body longitudinal axis (for an explanation of the chaetal formation process on the edge of rows and some modifications to this pattern see Hausen, 2005). Spionidae, *Magelona*, and Cirratulidae have transverse rows of chaetae in both parapodial rami of all chaetigers while in *Poecilochaetous* and *Trochochaeta* this chaetal arrangement is only found on anterior chaetigers. Transverse rows are present in neuropodia of Terebellida and Sabellidae but notochaetae are arranged in bundles, although this arrangement is inverted in the latter group on abdominal segments. Chaetal arrangement in Oweniidae has been interpreted as bundles in the notopodia (Parapar, 2003) and the patches of hooks in neuropodia as modified transverse rows (Hausen, 2005). Chaetal arrangement in *Sternaspis* is not yet fully understood (Beesley, Ross & Glasby, 2000; Rouse & Pleijel, 2001) and has been interpreted here as transverse rows of noto- and neurochaetae in the anterior segments (Petersen, 2000) but as the bundles on the posterior end could be noto-, neurochaetae or both (Rouse & Pleijel, 2001) it has been scored as a question mark herein.

Chaetal shape and ultrastructure (characters 26–40)

The diversity of chaetae and their arrangements is high among polychaetes and has been the issue of

several studies. Different interpretations have been suggested over the years (e.g. Bartolomaeus, 1995, 1998; Rouse & Fauchald, 1997; Hausen & Bartolomaeus, 1998; Hausen, 2005) and consequently suggesting in some cases dissimilar phylogenetic hypotheses. According to some authors homology can be assumed between subchaetal units for individual chaetae (e.g. Hausen, 2005). Therefore, for taxa bearing uncini, we have considered absence or presence of capitium, rostrum, subrostrum, subrostral process, manubrium, or basal process as independent characters and for those with chaetae, the presence of aciculae (non-protruding chaetae supporting parapodia), simple (spines or capillaries) or compound chaetae. We have also considered the presence and arrangement of a particular type of chaetae of anterior segments to incorporate those typical of the operculum in Sabellariidae and Pectinariidae (Dales, 1952; Orrhage, 1978; Rouse & Pleijel, 2001; Hutchings & Peart, 2002; Orrhage & Müller, 2005). Some Sabellariidae present thick spines, with straight or curved tips (hooks), formed in the sacs of the opercular paleae and considered as derived from segment 1 (Orrhage, 1978) but it is uncertain if they are noto- or neurochaetae. In some Ampharetidae hooks are present in the third or fourth segment (Beesley et al., 2000) and seem to be notopodial (Nogueira et al., 2010). Chaetae in the rest of chaetigers have been herein classified as spines (simple, thick chaetae regardless of shape), capillaries (simple thin chaetae), or compound chaetae (comprising two units, a shaft and a blade). Members of the outgroup have typically simple (Polynoidae) and compound (Nereididae) chaetae. All members of the ingroup have simple chaetae.

Unicini or hooks with rostrum or main fang are present in Terebellidae, Sabellidae and in the thoracic segments of Serpulidae and absent in the rest of taxa included in the present study (Bartolomaeus, 1995; Hausen, 2005). The rostrum has been interpreted as present in *Magelona* (as Rousset et al., 2004). A capitium, or teeth above main fang, is present in all taxa except for some Spionidae (Hausen & Bartolomaeus, 1998). A subrostrum or breast is absent in Oweniidae, *Magelona*, Pectinariidae, and Spionidae (Bartolomaeus, 1995; Hausen & Bartolomaeus, 1998) and all terminals except for some Serpulidae and Terebellidae have a manubrium. Basal process (as in Hausen, 2005) is present in Terebellida.

POSTERIOR SEGMENTS AND PYGIDIUM
(CHARACTERS 41–43)

There is some controversy about the segmented nature of the posterior region of sabellariids, the cauda, and some authors suggest that it be considered as segmented (Wilson, 1929) while others do not (Kirtley, 1994). This has not only morphological but phylogenetic implications (see Rouse & Fauchald, 1997). In the present study these two structures have been considered as different and not homologous as their morphology and function differ (see Watson, 1928). Pygidium is in some taxa provided with some cirri (Spionidae, *Poecilochaetous*, *Magelona*, and Pectinariidae).

SENSE ORGANS (CHARACTERS 44–51)

Most polychaetes possess prostomial eyes and are also called cerebral eyes (Char. 11) because of their proximity to the brain. Some Phyllodocida have multicellular (Char. 12) and lenticular eyes (Char. 13) absent in the rest of the groups (e.g. Suschenko & Purschke, 2009). Prostomial ocelli (Dales, 1952) are present in some sabellariid adults, in the area near the median ridge (e.g. Kirtley, 1994; Nishi & Núñez, 1999) or at the base of the palps. They seem to be a feature that is consistent within some genera although revisions should be made as they are not often mentioned in descriptions. Sabellids show a wide range of prostomial eyes from simple ocelli to compound eyes formed by groups of ommatidia and arranged in several positions of the radiolar crown (Suschenko & Purschke, 2009; Capa et al., 2011). In Terebellida, the presence of prostomial eyes is a variable condition and has been scored herein as present in *Sternaspis* (Petersen, 2000), some terebellids (Nogueira et al., 2010), and cirratulids but absent in *Magelona* (Wilson, 2000; Rouse & Pleijel, 2001) and adults of pectinariids (Thorson, 1946).

Nuchal organs are present in most polychaetes and they have been recently found in some taxa considered as not having them. In those remaining cases, as in Oweniidae, *Sternaspis*, or *Magelona* (Rullier, 1950, 1951; Rouse & Pleijel, 2001; Bartolomaeus et al., 2005; Lindsay, 2009), their absence is considered as a secondary loss (Purschke, 1997, 2005). Some polychaetes present large nuchal organs while in sabellids, serpulids, sabellariids, terebellids, or pectinariids these are reduced (Watson, 1928; Purschke, 1997). All nuchal organs exhibit similar ultrastructural components (e.g. Rullier, 1951; Purschke, 1990, 1997, 2005; Jelsing, 2003), with some exceptions such as Protodilidae where the cuticle has been replaced by a special cover (Rullier, 1951; Jelsing, 2003; Purschke, 2005). Nuchal organs of Sabellidae, Serpulidae, and Terebellidae are unpaired and in the former two groups they are in an uncommon position in the dorsal epithelium of the mouth cavity (Purschke, 1997, 2005). In sabellariids nuchal organs are located at the base of each palp (Johansson, 1927; Orrhage, 1978).

Lateral organs are known to occur and to present a similar structure and cellular composition in some of the taxa included in the present study, such as Ampharetidae, *Magelona*, Pectinariidae, *Poecilochaetus*, Spionidae, Terebellidae, and *Trochochaeta* (Purschke, 2005; Purschke & Hausen, 2007).

BRANCHIAE (CHARACTERS 52–54)

Segmental branchiae are present in most members of the ingroup. They sometimes arise from the parapodia (Sabellariidae and Pectinariidae) or epithelium of the dorsum of the body and are absent in the outgroup. They can be present in most segments (Cirratulidae), be restricted to only a few anterior (Spionidae, Ampharetidae, and most Terebellidae) or posterior ones (*Poecilochaetus*, *Sternaspis*). Sabellidae and Serpulidae do posses 'branchiae' but they are prostomial and *Trochochaeta* lack branchiae although some of the segmental papillae along the midventral line of the body have been erroneously interpreted as such (Rouse & Pleijel, 2001).

MUSCLES (CHARACTER 55)

The type of muscles (longitudinal, oblique, circular) and the arrangement shown amongst polychaetes have been suggested to be of interest for systematic and phylogenetic purposes (Tzetlin & Filippova, 2005; Purschke & Müller, 2006) but for many taxa no data are available. For the present study, we have considered the presence of the circular fibres because of some information available in the literature (Tzetlin & Filippova, 2005; Purschke & Müller, 2006). They are arranged in an almost complete cylinder interrupted only by the ventral nerve cord in some sedentary polychaetes and are less developed in nereidids and terebellids and suggested to be absent in *Magelona* and at least some spionids, oweniids, and polynoids (Tzetlin & Filippova, 2005; Purschke & Müller, 2006, and references therein).

ALIMENTARY CANAL (CHARACTERS 56–63)

Tzetlin & Purschke (2005) reviewed and updated the information regarding the alimentary canal of polychaetes. The anterior end of the gut or foregut is very variable among polychaetes due to adaptation to the environment and feeding strategies. In Sabellidae, Serpulidae, and Sabellariidae the foregut is simple and a buccal organ seems to be absent (Beesley *et al*., 2000; Rouse & Pleijel, 2001; Zrzavý *et al*., 2009). The types of buccal organs have been classified as a ventral pharyngeal organ (simple or with well-developed muscles), axial muscular pharynx or proboscis, axial non-muscular pharynx and dorsolateral

ciliary folds which can occur in combination with a ventral pharyngeal organ (e.g. Beesley *et al*., 2000; Rouse & Pleijel, 2001; Tzetlin & Purschke, 2005). A ventral pharyngeal organ is present in most Terebellida and also Oweniidae. An axial muscular pharynx is present in Phyllodocida (outgroup) and some have sclerotized structures such as jaws or paragnaths derived from the cuticle that covers the epithelium of the foregut (Tzetlin & Purschke, 2005). The proboscis in *Sternaspis* (Dales, 1962; Rouse & Fauchald, 1997; Tzetlin & Purschke, 2005) has also been interpreted as simple and axial.

The midgut or intestine is formed by a straight tube running along the body from the mouth to the anus in most polychaetes but in some groups it is coiled within the septa dividing each segment (Cirratulidae), forms one or two loops in the anterior part of the body (Ampharetidae, Pectinariidae) or it has lateral and dorsal branches (Polynoidae). Sabellariidae bears a swollen and thickened structure (Fig. 9D, E) in the abdominal region referred to a 'proventricle' (McIntosh, 1922) and a band of tissue is present in the mid-dorsum and sometimes mid-ventrum where the gut content can be seen through the body wall.

GULAR MEMBRANE (CHARACTERS 64–65)

The presence of this modified septum is characteristic of some Terebellida but its shape and arrangement differ between groups. In the present study the presence and position have been included as this membrane attaches to the body wall between the fourth and fifth segment in Terebellidae and Ampharetidae and between the third and the fourth in Pectinariidae (Zhadan & Tzetlin, 2003).

NEPHRIDIA (CHARACTERS 66–69)

The excretory organs in polychaetes have been classified as protonephridia or metanephridia according to their function. These organs do sometimes vary with developmental stage, the monociliated protonephridia being the potential primitive condition for the first pair of nephridia differentiated during development (head kidneys) in Annelida and the rest of segmental nephridia derived from those were metanephridia (for a review see Bartolomaeus & Quast, 2005).

Sabellariids, sabellids, and serpulids have a single anterior pair of excretory segmental organs (Meyer, 1887; Dehorne, 1952) and a posterior pair for discharging gametes (Meyer, 1887; Rouse & Fauchald, 1997). This is also the case for *Sternaspis* and cirratulids (Rouse & Pleijel, 2001). Pectinariids, ampharetids, and some members of Spionida and Terebellidae have more than one anterior segmental

organ acting as nephridia, in addition to posterior gonoducts, but there are some exceptions, such as members of *Pista* with only one single pair of nephridia (Rouse & Pleijel, 2001). The outgroup has segmental organs in most segments.

CIRCULATORY SYSTEM (CHARACTERS 70–72)

All taxa included in the analyses have a closed circulatory system. Some groups, such as Ampharetidae, Pectinariidae, Terebellidae, Cirratulidae, and Sabellariidae, have a heart body that forms blood (Dales & Pell, 1970; Rouse & Pleijel, 2001), probably homologous to the intravasal tissue found in serpulids (Hanson, 1951). Most polychaetes have acellular blood and therefore have developed other defence systems against infections. Exceptions are *Magelona* and *Pectinaria* (Kennedy & Dales, 1958; Rouse & Pleijel, 2001).

NERVOUS SYSTEM (CHARACTERS 73–74)

Most polychaetes have a subepidermal nervous system but there are some exceptions, such as the Oweniidae, included herein. Some annelids, generally the predators, have well-developed mushroom bodies, a brain centre innervating the palps (Heuer *et al.*, 2010; Loesel & Heuer, 2010) but some taxa still need to be investigated.

REPRODUCTIVE STRATEGY, FERTILIZATION, AND PARENTAL CARE (CHARACTERS 75–79)

The majority of polychaetes are gonochoric but examples of hermaphroditism have been documented and are not scarce (McIntosh, 1911; Tweedell, 1966; Schroeder & Hermans, 1975; Rouse & Fitzhugh, 1994; Giangrande, 1997). In the present study we have, in some cases, generalized for the genera if cases of specific terminals were not available. Most polychaetes spawn gametes freely into the sea water (Blake, 2006; Rouse, Kupriyanova & Nishi, 2006; Halt *et al.*, 2006) but some nereidids or polynoids do have pseudocopulation (Pettibone, 1963; Hsieh & Simon, 1990) and some spionids do transfer sperm in spermatophores (Rice, 1978; Hsieh & Simon, 1990). Polychaetes sometimes exhibit some sort of parental care or brooding of their eggs, larvae, or juveniles, like several sabellids, serpulids, and some spionids (Rouse & Fitzhugh, 1994; Blake, 2006; Rouse *et al.*, 2006), none of them included in this study.

GAMETOGENESIS (CHARACTERS 80–86)

Some aspects of oogenesis, such as structure and position of the ovary, the type of oogenesis, and the structure of the egg envelope appear to be conserved at family level among the polychaetes, with some exceptions and have been proposed as having potential phylogenetic use (Eckelbarger, 2005, 2006). Most polychaete ovaries are retroperitoneal and are generally located in some anterior segments (Terebellidae, Ampharetidae, Pectinariidae, *Polydora*) or in all segments along the body, but some families lack discrete ovaries, such as Nereididae (Eckelbarger, 2005). Sabellariids produce and store gametes in the coelomic cavity of the abdominal segments and gamete-containing segments of mature males appear whitish, while those of mature females are blue in colour. Some of the groups that show diversity of structure and position of the ovary are serpulids (Kupriyanova *et al.*, 2001). Oogenesis can take place in the ovary or in the coelom. Examples of intraovarian oogenesis are in members of Sabellariidae, while in Ampharetidae, Cirratulidae, *Polydora*, *Sternaspis*, Pectinariidae, Sabellidae, and Terebellidae the oocytes develop and grow outside the ovary and they leave this organ as individual previtellogenic cells (Pectinariidae and Sabellidae) or in clusters (Ampharetidae, Cirratulidae, Pectinariidae, Terebellidae) (Eckelbarger, 2005, 2006; Blake, 2006; Halt *et al.*, 2006). Mature eggs are surrounded by egg envelopes consisting of an extracellular matrix penetrated by microvilli, and in members or certain families such as Spionidae or Serpulidae this egg envelope can be ornamented (Blake & Arnofsky, 1999; Kupriyanova *et al.*, 2001; Eckelbarger, 2005).

The sperm of only a few taxa have been studied in detail but shape of the sperm varies among species (e.g. Franzén, 1956; Eckelbarger, 1976, 1984; Rouse, 2006a). *Sternapsis* and most cirratulids have short-headed sperm but there are some exceptions in cases of species that brood (Halt *et al.*, 2006). All sabellariids studied are gonochoric, broadcast spawners (Wilson, 1991). When animals are mature they have well-developed gonads throughout the year, suggesting that they are able to reproduce all year long, at least in some of the species studied (e.g. Eckelbarger, 1976).

LARVAL DEVELOPMENT AND LARVAL FEATURES (CHARACTERS 87–97)

Development is highly variable among polychaetes with examples of planktotrophic, lecithotrophic larvae and some with direct development even in closely related species (e.g. Terebellidae, Serpulidae, and Spionidae; Wilson, 1991; Giangrande, 1997; Rouse, 2003). Several characters reflecting the absence or presence of larval ciliary bands reviewed in detail (Rouse, 1999, 2006b; Pernet, 2003) have been incorporated in the analyses. Sabellariid larvae seem not to have a metratroch but a prototroch that overhangs the lateral edges of the mouth acting in a similar way

to a metratroch (Rouse, 2006b). All sabellariids have a long development in the plankton. Life-history studies on several species have demonstrated the great similarities in larval development between members of Sabellariidae (Wilson, 1929, 1991; Dales, 1952; Curtis, 1973; Eckelbarger, 1975, 1976, 1977, 1978). The common body organization in many of the species studied indicates a particularly homogenous developmental type at the family level (Bhaud & Fernández-Álamo, 2001). The main differences among early larvae are related to the size and colour pigments, but during later larval stages the development of chaetae, both spines and paleae, differ between species and have been using for taxonomic purposes in the past (Eckelbarger, 1976). They superficially resemble those of spionids (Caullery, 1914; Wilson, 1929; Dales, 1952).

TUBE (CHARACTERS 98–99)

The typical polychaete tube dwellers are members of Sabellida, Oweniidae, Terebelliformia, and Spionida but some other groups build tubes even if temporary, like most Nereididae. Within the ingroup most tube dwellers produce tubes made of mucus and attached sediment particles although members of Serpulidae typically build calcareous tubes.

APPENDIX 2

DESCRIPTION OF CHARACTERS FOR ASSESSING THE SABELLARIID PHYLOGENY

The body of sabellariids is divided up into four regions: the operculum, parathorax, abdomen and caudal region (Fig. 1).

OPERCULUM: HEAD AND THORAX (CHARACTERS 1–8)

The operculum (Figs 5A, B, 6A) is an elongate structure with two lateral fleshy lobes. Some genera have the opercular lobes completely fused (Fig. 7A), fused dorsally and with a deep ventral groove on the ventral margin (Fig. 7B) or completely separated (Fig. 7C). The relative length of the operculum varies among sabellariids but in most cases is consistent within genera (Fig. 7D, F). The distal end of the operculum, called a disc (Orrhage, 1978) or a crown (Kirtley, 1994; Rouse & Fauchald, 1997), bears rows of paleae and is surrounded by appendages called opercular papillae (Figs 5A, 7D–F). In most sabellariids this disc is oriented perpendicular to the longitudinal axis of the body (Fig. 8A), although in some genera it is oriented in an oblique position, often described as having a distal end sloped posteriorly to midline (Kirtley, 1994; Fig. 8B). The number and

shape of opercular papillae (Fig. 3C) is species specific and it has sometimes been used for taxonomic purposes.

On the ventral and inner side of each opercular lobe, other appendages may be inserted, referred herein to as tentacular filaments (Hartman, 1944; Dales, 1952; Kirtley, 1994; Figs 5, 6) or oral filaments according to some authors (Orrhage, 1978) and seem to be a synapomorphy for the family (Rouse & Pleijel, 2001). These are ciliated, and often grooved proximally and involved in the transport of food particles to the mouth (Dales, 1952; Orrhage, 1978; Dubois *et al.*, 2005; Riisgård & Nielsen, 2006). Tentacular filaments can be simple (unbranched, Fig. 2D) or compound (branched, Figs 2E, 3D, E). In some species, the oral filaments are replaced by elongate tentacular buccal flaps or oral plates (Figs 7F, 8F) or by apophyseal ridges along the posterior–lateral margins of the buccal cavity (Kirtley, 1994).

A pair of grooved and ciliated palps (Figs 5B, 7D–F, 8E, G–H; Treadwell, 1926), also referred to as prostomial or pretentacular filaments (Dales, 1952; Kirtley, 1994) or other terms (see a summary in Orrhage, 1978), arise from behind the prototroch (Dales, 1962), on the anterior margin of the upper transverse lip, in front of and dorsal to the mouth (Johansson, 1927; Orrhage, 1978) and therefore are considered herein as peristomial. The relative length of the palps and operculum has been considered in this study as a variable character among groups of sabellariids, although it has been indicated to be contractile (Treadwell, 1926). In some sabellariids an unpaired appendage, called median organ (Figs 5B, 8H–K), median cirrus, preoral lobe (Caullery, 1944), or tentacule (Gravier, 1909) with sensory function is present at the dorsal junction of the opercular lobes (Kirtley, 1994).

OPERCULAR CHAETAE (CHARACTERS 9–25)

The opercular paleae arise in two separate chaetigerous sacs (Ebling, 1945; Dales, 1952; Orrhage, 1978) forming two distinct series of paleae, and outer and an inner row, on each lobe (Hartman, 1994). The orientation of the distal blades sometimes gives the appearance of animals presenting three concentric rows of paleae, where both the inner and the median row are formed from the inner chaetigerous sac (Kirtley, 1994). In those cases, the blades of paleae from the median and inner row can be both directed inwards (Fig. 7G) or, the inner paleae can be directed inwards and the median paleae outwards (Fig. 7H). For the present study we have considered the total number of paleae in the outer and inner row as separate characters in the matrix. The outer paleae are generally arranged in facing semicircles but this arrangement varies in some

species where outer paleae display a spiral arrangement (Fig. 7I). Opercular paleae show a great diversity in number, shape and size. We have followed the convention (Ebling, 1945; Kirtley, 1994) of referring to the proximal end, which is attached to the muscular tissue, as the paleal shaft and to the distal exposed end, which is normally ornamented, as the blade (Fig. 7J). All paleae appear to consist of two distinct regions, an inner core and an outer layer also referred to as thecae (e.g. Kirtley, 1994). The inner core is striated longitudinally and the outer layer (cortex or thecae) is clear and homogeneous, forming an even covering around the shaft and relatively thinner in the blade region, with more or less packed fibres or microtubules (Ebling, 1945). In some paleae an alveolar structure can be seen, consisting of gas-filled cavities arranged in longitudinal and transverse rows. Opercular paleae are replaced during metamorphosis and subsequent adult growth, changing its shape during ontogeny. In larval stages (features retained in some adults), they have been classified as choanothecae, hemithecae, and platythecae depending on the shape of the section of the blade (for a description of different types see Kirtley, 1994). The terminology used for describing paleae in the literature is highly varied. In this study, we have selected some characters such as the overall shape of the blade, the ornamentation of lateral and distal margins, and angle of the blade to the longitudinal axis of the shaft. We have avoided subjective terms common in the literature and we have not scored the fine details of the thecae types, microsculpture, internal striation, frayed denticles, curved denticles, shape of shafts, or colour as these are features that are highly variable within genera and sometimes even within species. The types of paleae considered in the present study are summarized as follows: the angle of the longitudinal axis of blades and shafts and if they are straight (Figs 7K, 10A, C–F) or geniculate chaetae (Figs 7L, 10B); regarding the shape of the blade whether they are flat (Figs 7M, 10D–G), concave (Figs 7N, 10H), or cylindrical (Figs 7O, 10C); regarding the shape of the lateral margins and whether they are smooth (Figs 7P, 10D) or denticulate (Figs 7K, 10E, F) chaetae; and regarding the distal ends, some exhibit smooth edges (Figs 7P, 10D) and others have denticles (Figs 7M, 10E–G).

Some sabellariids have thick cylindrical and pointed chaetae on the dorsal edge of the opercular lobes called nuchal spines (Figs 5B, 9A, 10I, J). These can have straight or bent distal tips (also known as nuchal hooks) (Fig. 7Q–S). They are formed in the sacs of the opercular paleae, and are therefore considered as derived from segment 1 (Orrhage, 1978). The number of spines and hooks varies among genera and species and the presence of a more or less devel-

oped limbation (e.g. Fig. 7S) on inner or outer margin of the hooks also characterizes some taxa.

THORAX (CHARACTERS 26–29)

There is a pair of small neuropodia (Figs 5B, 8D, F–H, M) at the lateral sides of the building organ and the mouth with conical cirri, which number is of taxonomic use. In most taxa chaetae are regarded as the neurochaetae of the first segment (Kirtley, 1994; Fig. 8G, J). The second thoracic segment bears neuropodial cirri and bundles of capillary neurochaetae with thecae (coanotheace and hemithecae) make them appear as bipinnate (as referred by Kirtley, 1994). Thoracic notopodia do not have chaetae but in some taxa, dorsal cirri (one to three), referred herein as lateral lobes may be present (Fig. 9B, C). Branchiae can be present or absent in segment 2 and, in most cases, is a generic feature.

PARATHORAX (CHARACTERS 30–31)

Behind the thorax are either three or four parathoracic segments which are biramous. Neuropodia are conical and notopodia are enlarged lobes. Notopodia bear stout chaetae with lanceolate tips and cylindrical capillary chaetae alternating in one row, although chaetae in neuropodia are smaller in size (e.g. Kieselbach & Hausen, 2008). In some genera the lanceolate chaetae are frayed or denticulated at the tips. Neuropodia show higher variation between taxa and some species have both lanceolate chaetae and capillaries (Fig. 10K) while other only bear capillaries or only lanceolate chaetae (Fig. 10L). All segments have paired conical and weakly ringed branchiae (Figs 5A, 6B, 9A). Glandular areas are present on the ventrum of this region and they produce cementing and fixative substances for building the tube (Vovelle, 1965 in Kirtley, 1994).

ABDOMEN

Parathoracic and abdominal segments can be easily separated by the presence of uncini in the notopodia. Some authors indicate an absence of lanceolate neurochaetae, and only presence of capillaries in this region, although a gradual change has been observed in some species (Kieselbach & Hausen, 2008). Abdominal segments are biramous, with conical neuropodia bearing conical ventral cirri and fascicles of chaetae and notopodia as transverse tori, with a single row of uncini, diminishing in size posteriorly. Neurochaetae are capillary (often with well-developed thecal sculpture, Fig. 10M) arranged in one or two rows with two separated formation sites (Kieselbach & Hausen, 2008) and notochaetae are pectinate

uncini with series of similar-sized denticles pointing anteriorly (Fig. 10N). Cirri are present between the two noto- and neuropodia rami (Kieselbach & Hausen, 2008). Branchiae are present in most or only on anterior abdominal segments and they decrease in size towards the posterior end (Figs 5B, 9F). No abdominal features have been selected for the analyses because the morphological variation is specific more than generic.

CAUDA

This region is formed by an apparently unsegmented (although there are other opinions, Wilson, 1929), smooth, cylindrical tube that is curved along the ventral surface of the abdomen (Figs 5A, B, 9F). No features from this region have been selected for the analyses due to small variation between taxa.